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Fishery Bulletin

U.S. Department of Commerce
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Under Secretary for Oceans and Atmosphere

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Larval development of *Symphurus williamsi* (Cynoglossidae: Pleuronectiformes) from the Gulf of California

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Abstract.—The larval development of *Symphurus williamsi* Jordan and Culver, 1895 (Cynoglossidae: Pleuronectiformes) is described from 69 specimens from the Gulf of California, Mexico. Diagnostic characteristics used to identify larvae of this species are 3–5 pigment spots situated on the dorsal region of the body of the base of the pterygiophore of the dorsal fin and 3–4 pigment spots on the ventral region of the body on the base of the pterygiophore of the anal fin. In early stages, a pigment is present on the base of each anal-fin ray. These pigments also appear at the bases of the dorsal-fin rays in the posterior third of the dorsal fin. The first three dorsal-fin rays are elongated in larvae less than 11.2 mm body length.

Symphurus is a world-wide genus distributed predominantly in temperate and tropical seas and oceans. The genus has 71 recognized species, 17 of which are found in the American region of the Pacific Ocean (Munroe, 1992). Thirteen species have been found in the Gulf of California: *S. atramentatus*, *S. atricaudus*, *S. callopterus*, *S. chabanaudi*, *S. elongatus*, *S. fasciolaris*, *S. gorgonae*, *S. leei*, *S. melanurus*, *S. melasmatotheca*, *S. oligomerus*, *S. prolatinaris*, and *S. williamsi* (Munroe and Mahadeva, 1989; Munroe, 1990; Munroe and Nizinski, 1990; Mahadeva and Munroe, 1990; Munroe et al., 1991; Munroe et al., 1995). Specimens of *Symphurus* are usually captured in large quantities by shrimp trawls in some tropical regions, but they are not exploited commercially because of their relatively small size (Pérez and Findley, 1985; Van der Heiden, 1985; Van der Heiden et al., 1986).

The taxonomy of the eastern Pacific species was poorly defined until the recent study of Munroe (1992), who concluded that it was possible to identify each of these species by a combination of the dorsal-, anal-, and caudal-fin ray counts and by the interdigitation patterns of dorsal proximal pterigyophores and neural spines (ID pattern).

Symphurus williamsi Jordan and Culver, 1895, can be found from the southern region of the Gulf of California, Mexico, to Panama in shallow waters with sandy bottoms (Munroe et al., 1995). Larvae occur throughout the Gulf of California. Large numbers were found during the summer in collections made south of Islas Tiburón and Angel de la Guarda (Aceves, 1992).

Of all species found in the American region of the Pacific, only the larvae of *S. atricaudus* (the only species of this genus distributed north as far as California) and *S. elongatus* have been described (Moser, 1981; Ahlstrom et al., 1984; Matarese et al., 1989; Charter and Moser, 1996). In this study, we offer a description of the larval stages of *S. williamsi* from preflexion through prejuvenile stages. Observations made on the larval development of *S. williamsi* are compared with those made previously on *S. atricaudus* and *S. elongatus*.

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Table 1

Meristics for species of *Symphurus* of the Gulf of California with the same pterygiphore interdigitation pattern (1-5-3-2-2) taken from Munroe (1992).

	S. williamsi	*S. atricaudus*	*S. chabanaudi*	*S. elongatus*	*S. melasmatotheca*	*S. melanurus*	*S. prolatinaris*
Dorsal-fin rays	89–95	94–102	98–109	99–107	90–98	96–104	103–110
Anal-fin rays	73–79	77–83	82–92	83–90	74–80	79–87	86–93
Caudal-fin rays	12	12	12	12	11	12	12
Total vertebrae	47–51	50–53	52–57	53–56	49–52	50–54	54–58

Materials and methods

Plankton samples were taken during eight oceanographic expeditions made in the Gulf of California in April, July–August, and November–December 1984, June and August 1986, July 1991, September 1993, and June 1994. Samples were obtained by using oblique tows with 60-cm diameter bongo nets equipped with nets of 333-µm and 505-µm mesh, as detailed in Kramer et al. (1972). All larvae and juveniles used in this study were deposited in the larval fish collection of the Plankton and Marine Ecology Department of Centro Interdisciplinario de Ciencias Marinas of the Instituto Politecnico Nacional (CICIMAR-IPN).

All *Symphurus* larvae collected with the 505-µm net were separated from the other net contents. Flexion, postflexion, and juvenile specimens were cleared, stained (Potthoff, 1984), and identified on the basis of meristic characteristics (Munroe, 1992). Subsequently, a developmental series of preflexion larvae showing similar pigmentation patterns and meristic features was assembled. Counts of the dorsal- and anal-fin elements were sometimes extrapolated from pterygiophore counts, which occasionally appeared earlier in development than did corresponding rays. The following measurements were done on the left side of the body of the specimens:

Body length (BL): anterior end of snout to end of notochord in young larvae, or to posterior margin of hypural plate in more developed larvae.

Head length (HL): anterior end of snout to cleithral margin in small specimens, or to posterior margin of the opercle in larger ones.

Snout-anus length (Sn-A): anterior end of snout to posterior margin of anus.

Body depth (BD): vertical distance between dorsal and ventral margins (dorsal- and anal-fin pterygiophores excluded) at origin of pelvic fin.

Body depth at anus (BDA): vertical distance between dorsal and ventral margins (dorsal- and anal-fin pterygiophores excluded) at origin of anal fin.

Eye diameter (ED): horizontal distance between anterior and posterior margins of left eye (Moser, 1996).

The description of larval development was based on 69 specimens (2.2–13.2 mm BL). None of these larvae were in the yolksac stage, indicating that eclosion must have taken place at a smaller size. To characterize larval development intervals, divisions proposed by Ahlstrom et al. (1976) were followed.

Results

Cleared and stained larval and prejuvenile specimens (n=17, between 7.7–13.2 mm BL) showed the following pterygiophore patterns: 1-5-3-2-2 (41.2%), 1-5-2-3-2 (35.2%), 1-5-2-2-2 (11.8%), 1-4-2-2-2 (5.9%), and 1-5-4-2-2 (5.9%). There are seven species in the area with the same main pterygiophore pattern (Table 1). Using these 17 specimens and the remaining 52 larvae (Table 2), we counted 9 precaudal vertebrae, 38–42 caudal vertebrae (mode=40), 89–97 dorsal rays (mode=92 and 94), 71–80 anal rays (mode=75), and 12 caudal-fin rays. The combination of these characteristics indicates that the species is *S. williamsi*.

Description of the larvae

Diagnosis *Symphurus williamsi* larvae typically have a pigmentation pattern of 5 spots along the middorsal line at the bases of the dorsal-fin pterygiophores and 2 to 3 similar spots located on the bases of the dorsal-fin rays. There are also 3 to 4

Table 2

Symphurus williamsi larvae and juvenile measurements (mm): body length (BL), snout-anus length (Sn-A), head length (HL), eye diameter (ED), body depth (BD), body depth at anal fin (BDA), and individual counts: dorsal rays (DR), anal rays (AR), caudal rays (CR), caudal vertebrae (CV), and total vertebrae (TV). Start of flexion stage (═══); start of postflexion stage (- - -); start of juvenile stage (——).

BL	Sn-A	HL	ED	BD	BDA	DR	AR	CR	CV	TV
2.2	1.1	0.6	0.2	0.5	0.3				22	31
2.4	1.1	0.6	0.2	0.5	0.3				37	46
2.6	1.1	0.6	0.2	0.7	0.3				32	41
2.8	1.2	0.7	0.2	0.9	0.6				38	47
2.8	1.2	0.7	0.2	0.8	0.4				34	43
2.9	1.3	0.7	0.2	0.9	0.7				40	49
3.1	1.5	0.8	0.2	1.1	0.7				38	47
3.2	1.4	0.9	0.2	1.2	0.8				39	48
3.3	1.7	1.1	0.2	1.4	1.1				38	47
3.5	1.5	0.9	0.2	1.1	0.7				40	49
3.7	1.5	1.1	0.2	1.3	0.9				40	49
3.8	1.8	1.1	0.2	1.2	0.9				38	47
4.0	1.9	1.2	0.2	1.3	0.9				38	47
4.1	1.9	1.3	0.2	1.4	1.1				40	49
4.3	1.9	1.1	0.3	1.6	1.2				40	49
4.3	1.9	1.1	0.3	1.6	1.1				40	49
4.5	2.1	1.2	0.2	1.8	1.1				41	50
4.6	2.0	1.3	0.2	1.5	1.2				40	49
4.8	1.8	1.1	0.2	1.5	0.9				39	48
5.0	2.0	1.2	0.3	1.7	1.4				39	48
5.0	1.9	1.2	0.2	1.7	1.1				40	49
5.0	2.1	1.3	0.3	1.6	1.2				38	47
5.3	2.1	1.4	0.3	1.7	1.2				40	49
5.6	2.0	1.4	0.3	1.5	1.1				41	50
5.8	2.3	1.5	0.3	1.9	1.4				40	49
5.9	2.3	1.4	0.3	1.9	1.2				40	49
6.1	2.4	1.6	0.3	1.9	1.5				40	49
6.1	2.2	1.7	0.3	1.9	1.4		80		40	49
6.3	2.4	1.5	0.3	1.8	1.4				40	49
6.6	2.2	1.6	0.3	2.1	1.5				38	47
6.8	2.5	1.7	0.3	2.3	1.5	92	79		41	50
7.0	2.6	1.6	0.3	1.9	1.5	92	77		41	50
7.2	2.7	1.8	0.3	2.2	1.7	92	75		40	49
7.3	2.7	1.7	0.3	1.9	1.5	95	79		40	49
7.4	2.5	1.7	0.3	2.3	1.5	94	75		41	50
7.7	2.6	1.7	0.3	2.0	1.7	92	75	12	40	49
7.8	2.9	1.9	0.3	2.0	1.6	94	76	12	38	47
8.0	2.8	2.0	0.3	2.2	1.7	93	77		41	50
8.2	2.8	1.9	0.3	2.3	1.9	96	77	12	40	49
8.3	3.1	2.0	0.3	2.4	1.9	95	76	12	41	50
8.3	2.9	1.9	0.3	2.4	1.8	96	79	12	40	49
8.3	2.9	1.9	0.3	2.3	1.9	93	76	12	40	49
8.4	3.0	1.9	0.3	2.1	1.5	94	76	12	39	48
8.7	2.9	2.2	0.3	2.5	2.1	91	74	12	40	49
9.3	3.0	2.1	0.3	2.0	1.6	94	75	12	38	47
9.5	3.3	2.2	0.3	2.3	2.0	94	77	12	40	49
9.6	3.4	2.2	0.3	2.6	2.1	91	75	12	38	47
9.8	3.1	2.0	0.3	2.3	2.0	92	76	12	40	49
9.9	3.2	2.1	0.3	2.2	2.0	93	71	12	39	48
9.9	3.2	2.1	0.3	2.3	2.1	94	78	12	41	50
10.0	3.0	2.2	0.3	2.5	2.2	91	75	12	40	49
10.2	2.8	2.2	0.3	2.4	2.2	92	75	12	41	50

continued

Table 2 (continued)

BL	Sn-A	HL	ED	BD	BDA	DR	AR	CR	CV	TV
10.4	3.1	2.2	0.4	2.5	2.3	92	76	12	41	50
10.6	3.4	2.3	0.4	2.3	2.1	93	74	12	38	47
10.6	3.3	2.3	0.3	2.2	2.2	91	75	12	39	48
10.7	3.5	2.2	0.3	2.6	2.3	94	76	12		
10.8	3.3	2.5	0.4	2.6	2.4	91	73	12	39	48
11.1	3.4	2.4	0.3	2.5	2.2	94	77	12	39	48
11.1	3.6	2.5	0.3	2.7	2.7	90	75	12	38	47
11.1	3.7	2.6	0.3	2.4	2.4	97	80	12	39	48
11.1	3.7	2.5	0.3	2.4	2.4	93	76	12	42	51
11.3	3.5	2.5	0.3	3.0	2.3	92	77	12	39	48
11.4	3.3	2.3	0.3	2.5	2.3	94	79	12	40	49
11.7	3.4	3.2	0.4	3.5	3.3	93	73	12		
11.9	3.8	2.8	0.3	2.5	2.3	92		12	40	49
12.7	3.2	2.5	0.4	2.3	2.7	91	75	12	38	47
12.9	3.9	3.0	0.3	2.4	2.6	89	74	12	39	48
13.1	3.9	3.0	0.3	3.1	2.4	94	74	12		
13.2	3.4	2.9	0.3	2.2	2.9	92	75	12	39	48

spots along the midventral line at the bases of the anal-fin pterygiophores, and 1 to 2 similar spots located on the anal-fin ray bases. At time of formation of the anal-fin rays, a melanophore appears at the base of each fin ray. A similar pigment is also found at the base of each dorsal- fin ray in the posterior third of the body in larvae less than 11.2 mm BL. The first 3 dorsal rays are elongated in larvae less than 11.2 mm BL, with the second and third of these longer than the first.

Morphological features The body is compressed and ribbonlike and has a deep head. The gut extends beyond the ventral profile. The intestine is noticeably coiled and its terminal end is directed towards the right side of the body. Larvae attain the appearance of juveniles when the protruding gut is incorporated within the ventral body profile at approximately 12 mm BL. At metamorphosis, a fleshy rostral beak is formed anterior to the dorsal-fin origin.

Migration of the right eye starts at 6.1 mm BL and eye migration is completed in larvae of 11.1 mm BL. The migrating eye crosses anterior to the dorsal-fin origin, between the rostral beak and the interorbital region. Notochord flexion begins at 5.0 mm BL and is completed near 8.0 mm BL. The juvenile stage begins at about 11.9 mm BL (Table 2).

Growth is not isometric throughout larval development (Table 3). Head length, snout-anus length, and body depth decrease with respect to body length from preflexion to juvenile stages. Body depth at the anal-fin origin remains constant throughout development. Eye diameter in relation to head length decreases from preflexion to juvenile stages.

Table 3

Symphurus williamsi larvae and juvenile body proportions (in percent of BL): body length (BL), head length (HL), snout-anus length (Sn-A), body depth (BD), body depth at anal fin (BDA), and eye diameter (ED).

Body proportions	Average	Standard deviation	Interval
HL:BL			
Preflexion	27	2.8	23–33
Flexion	25	1.3	23–28
Postflexion	23	1.5	20–27
Juvenile	22	1.4	20–24
Sn-A:BL			
Preflexion	45	3.3	38–52
Flexion	38	2.2	33–42
Postflexion	33	2.4	28–37
Juvenile	29	2.6	25–32
BD:BL			
Preflexion	33	5.2	21–42
Flexion	31	2.5	26–34
Postflexion	25	2.6	21–30
Juvenile	20	2.5	17–24
BDA:BL			
Preflexion	22	5.5	12–33
Flexion	23	2.0	20–28
Postflexion	22	2.0	17–28
Juvenile	20	1.3	18–23
ED:HL			
Preflexion	24	6.2	15–33
Flexion	19	2.5	15–25
Postflexion	14	1.8	12–18
Juvenile	11	2.3	10–12

Formation of scales begins at 7.7 mm BL over the cephalic region, and by about 10.3 mm BL, scales are evident over the entire body.

Pigmentation Early preflexion larvae typically have three melanophores along the middorsal line and two or three on the dorsal-fin fold. Three other melanophores are present along the midventral line, and one or two similar spots are found on the anal-fin fold. A melanophore is located over the coiled intestine in anterior and posterior positions. The ventral surface of the coiled intestine shows numerous smaller and dispersed melanophores. Two other melanophores appear in the anterior region: one on the cleithrum near the base of the pectoral bud; the other on the ventral margin of the preopercle. The dorsal surface of the swimbladder is also pigmented (Fig. 1A).

With finfold disappearance (late preflexion larvae), the characteristic pigmentation pattern is established: five spots located along the middorsal line at the bases of the dorsal-fin pterygiophores and two or three spots on the bases of dorsal-fin rays. Three or four spots appear along the midventral line at the bases of the anal-fin pterygiophores, and one or two spots are present on the bases of anal-fin rays.

When formation of the dorsal- and anal-fin rays is complete, a pigment spot appears on the base of each anal ray. Similar pigments are found on the bases of the fin rays in the posterior third of the dorsal fin. On the head, an inner melanophore appears over the forebrain and another over the otic region. Finally, a melanophore is present on the distal margin of the peduncle of the pectoral fin (Fig. 1B).

During the flexion stage, the pigmentation pattern of preflexion larvae remains, but the spots on the bases of anal- and dorsal-fin rays sometimes disappear. The pigment over the otic region, that on the opercle margin, and the melanophore on the posterior part of the intestine also disappear. In this stage there are additional pigments that appear. A series of dots are found over the ventral margin of the head, and a melanophore appears over the inferior portion of the base of the ventral fin. Flexion larvae are similar to those of postflexion larvae (Fig. 2A).

At the postflexion stage, three melanophores appears on the bases of the caudal-fin rays, and at 11.2 mm BL, the cephalic and opercular pigments may disappear (Fig. 2A).

In early juveniles, four spots appear on the midline of the body. Their positions with respect to the melanophores already present on the dorsal margin are one between second and third spots, one between third and fourth, one directly ventral to the fourth spot, and one posterior to the fourth spot. There is now pigment on the base of every dorsal-fin ray throughout the entire fin. A series of small spots also develop on the rays on the anterior part of the anal fin (Fig. 2B).

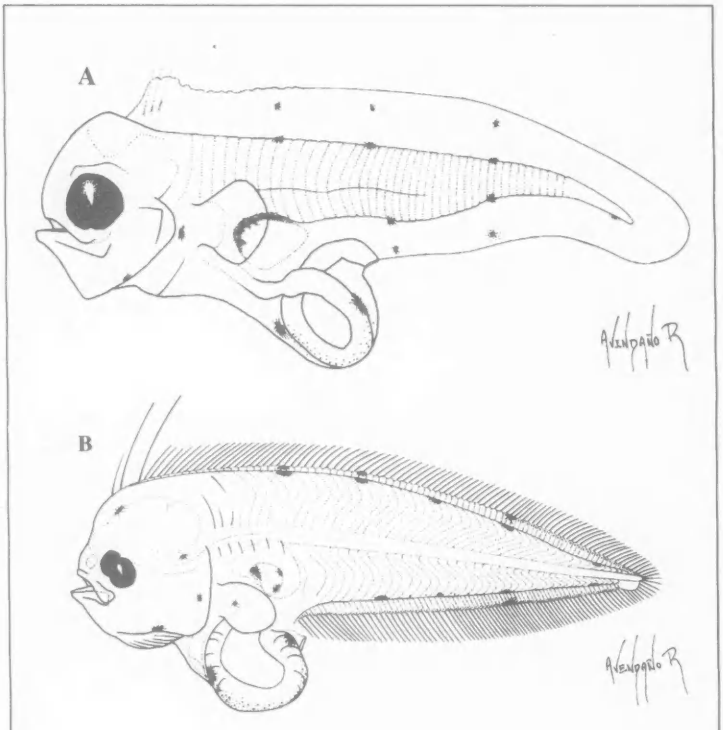

Figure 1
Symphurus williamsi: (**A**) 2.2-mm preflexion larva; (**B**) 6.3-mm flexion larva.

Fin formation

Unpaired fin development Incipient dorsal-fin rays are present in the anterior dorsal finfold at 2.8 mm BL. At 4.0 mm BL, about one half of the dorsal and anal rays are formed in a posterior direction. Complete formation of these fins occurs at about 6.8 mm BL. The 3 elongated dorsal-fin rays, present since this fin originated, disappear at 11.4 mm BL.

Paired fin development Pectoral-fin buds are present in the smallest lar-

vae we have seen (2.2 mm BL). This fin is reabsorbed at the postflexion stage (10.3 mm BL). Pelvic fins are developed at 5.7 mm BL. Only in early juveniles is a blindside pelvic fin located on the midventral line and the ocular pelvic fin is in a more dorsal position.

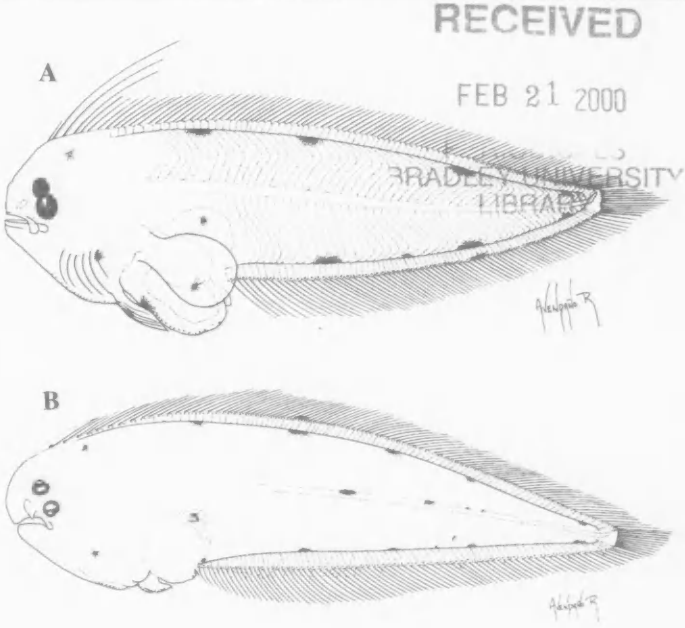

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Figure 2
Symphurus williamsi: (**A**) 10.0-mm postflexion larva; (**B**) 11.9-mm transformation larva.

Discussion

Larvae of *S. williamsi* are easily distinguishable from those of *S. atricaudus* by differences in pigmentation patterns. During early preflexion stage, *S. williamsi* has two or three pigments over the dorsal and midventral lines, and the pigments over the finfold are in the middle. *S. atricaudus* has a series of small melanophores along the midventral line. The pigments over the finfold are in blotches and are on the ventral and dorsal margins. There are also several pigments over the ventral margin of the head and the gut that *S. williamsi* does not have.

At the flexion stage, *S. williamsi* has the spot pattern along the dorsal and ventral profile. In contrast, *S. atricaudus* has a series of melanophores along the dorsal- and anal-fin margins and a series of pigments along the midbody line that never develop in *S. williamsi*.

In *S. williamsi*, three elongated rays are characteristic. In *S. atricaudus*, five rays appear first in the dorsal fin but never become elongated. The intestine in *S. williamsi* projects only ventrally, whereas in *S. atricaudus* the projection is ventroposterioriad.

Larvae of *S. williamsi* can be distinguished from those of *S. elongatus* by the pigmentation patterns. In the preflexion stage, *S. elongatus* does not have spots at the bases of the dorsal-fin rays, and these larvae do not have pigments at the bases of each of the anal- and dorsal-fin rays. Later in their development, the pigmentation of *S. elongatus* consists of a few distal pigments on the anal fin, twelve dashes along the lateral midline, and a small blotch on the caudal-fin rays, not observed in *S. williamsi*. In the early transformation stage, *S. elongatus* has a series of melanophores over the anterior part of the head, which never appear in *S. williamsi*. Like *S. atricaudus*, *S. elongatus* never develops elongated rays.

Yevseyenko (1990) described *Symphurus* sp. larvae. Its meristic characters have led us to believe it is *S. callopterus*, principally because of its ID pattern. These larvae are different from those of *S. williamsi* in pigmentation pattern because on the caudal section of the body an accumulation of pigment in the form of two oblique bands and two belts are found. These pigments are approximately equidistant from one other and never are found in *S. williamsi*.

Instead of three elongated dorsal-fin rays, like *S. williamsi*, *Symphurus* sp. have the first 7 dorsal-fin rays elongated from 7.5 to 25.4 mm BL (Yevseyenco, 1990). The presence of elongated fin rays in pleuronectiform larvae has phylogenetic interpretations only in bothids and appears to be apomorphic within the order and this family (Hensley and Ahlstrom, 1984). However the use of this characteristic for phylogenetic interpretations in cynoglossids does not allow proper comparisons because most larvae remain unknown.

Adults of *S. williamsi* (7.5 to 11.6 cm BL) are smaller than those of *S. atricauda* (13 to 18 cm BL)

and *S. elongatus* (13.5–15 cm BL) (Munroe et al., 1995), and this size difference is observed in larvae also. All stages of development in *S. williamsi* occur at smaller sizes (flexion between 5.0 and 8.0 mm and transformation >11.9 mm) than in other species. The flexion stage in *S. atricaudus* occurs between 8.6 and 10.8 mm BL (Ahlstrom et al., 1984; Matarese et al., 1989), and the transformation stage between 19 and 24.2 mm BL (Kramer, 1991). The flexion stage in *S. elongatus* is >6.8 mm and <18.9 mm BL and transformation takes place from >18.9 mm to <28.3 mm BL (Charter and Moser, 1996). In *Symphurus* sp. transformation occurs between 21 and 38 mm BL (Yevseyenko, 1990).

Usually the size range at metamorphosis that is plesiomorphic for the order is ca. 10 to 25 mm BL because most pleuronectiforms metamorphose in this range (Hensley and Ahlstrom, 1984).

Metamorphosis in *S. williamsi* occurs at ca. 11.9 mm BL; however, as described by Hensley and Ahlstrom (1984), size at metamorphosis is an important characteristic for larval identification, but its use for inferring phylogenetic relations in most instances is premature.

Symphurus williamsi has a larger head at all developmental stages, compared with those of *S. atricaudus* and *S. elongatus*. The distance from snout to anus in *S. williamsi* is relatively longer than it is in *S. atricaudus* but is similar to that of *S. elongatus*. In the juvenile stage, this distance is longer in *S. williamsi* than it is in *S. elongatus*. Larvae of *Symphurus* sp. as described by Yevseyenko (1990) have an abdominal cavity extending downward. This projection has the form of a greatly elongated sac, and the lower end terminates in a wormlike process that *S. williamsi* does not have. The loop of the intestine in *Symphurus* sp. is almost one half of the body length.

The body depth at the preflexion stage is greater in *S. williamsi* compared with that in *S. atricaudus* but is similar to that of larvae of *S. elongatus*. In postflexion and prejuvenile stages, this proportion is smaller in *S. williamsi* than in both of these other species.

Finally, body depth at the anus is shallower in *S. williamsi* than it is in *S. elongatus* at all stages in *S. atricaudus* during flexion and juvenile stages.

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Catchability estimates and their application to the red grouper (*Epinephelus morio*) fishery of the Campeche Bank, Mexico

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Abstract.—We applied a length-based additive catchability model that accounts for several sources of variation, namely time (i.e. years, months), density-dependence effects, and different fishing fleets. The model is based on 1) a transition matrix and 2) population length-structured data expressed as catch per unit of effort. Other sources of variation were estimated as anomalies from the average pattern and incorporated as additions to the slope of the catchability-at-length equation. The catchability model was applied to the red grouper (*Epinephelus morio*) fishery of the north continental shelf of Yucatan, a demersal fish resource exploited by three different fleets. A sigmoidal shape catchability-at-length function was fitted on the basis of grouper population biology and behavior, particularly reproductive aggregation. Catchability of immature fish was constant but increased with size for adult fish, especially during the reproductive season. Time- and density-dependent catchability responded to reproductive behavior and the allocation of fishing effort. When differences between fleets were incorporated, catchability differences emerged. The catchability model has the ability to identify the main properties of the fish resource and fishery that affect the relation between fishing effort and population abundance; it may therefore be helpful as an alternative stock assessment tool.

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Catchability has been considered in fisheries science as a parameter in the catch equation that relates fishing effort to population abundance:

$$C = qsEN, \qquad (1)$$

where C = catch in numbers;
q = catchability;
s = probability of gear selection;
E = fishing effort; and
N = the stock size in numbers.

From this relation it is easy to understand the key role of q. Because s and E are controlled by man, changes in population abundance will be reflected in catch through q. Although classically considered a constant, q represents different sources of variation affecting stock size. Most of the existing catchability models deal with only one source of variation related to schooling of fish (e.g. MacCall, 1976; Csirke, 1988, 1989), although a few of them also consider environmental factors (Table 1).

Investigations on catchability have developed mainly in two directions (Arreguín-Sánchez, 1996): 1) those related to measuring and increasing gear efficiency, and 2) those that use catchability as a parameter to relate fishing effort to fishing mortality and population abundance for stock assessment and management purposes. The aim of this contribution is to apply a catchability model that accounts for several sources of variation related to fishing and to population processes, as proposed by Arreguín-Sánchez (1996).

The red grouper (*Epinephelus morio*) stock over the Campeche Bank is one of the largest in the world, distributed on a continental shelf of more than 100,000 km^2. As with many serranids, the red grouper stock over the Campeche Bank, Gulf of Mexico, aggregates for reproduction, a fact that is well documented in the literature (Arreguín-Sánchez et al., 1996). While they aggregate, these fish are highly vulnerable to fishing; therefore this fish behavior is a key aspect for management of the resource. Three fleets target this fish species: two from Mexico (an artisanal and a midsize fleet); and a third from Cuba. These fleets do not completely overlap in respect to their fishing grounds, and their catch structure, efficiency, and the fishing mortality that they cause to the stock are different. Our contribution is aimed to estimate catchability for the red grouper fishery.

Table 1

Catchability models in literature accounting for more than one source of variation.

Catchability model	Comments	Reference
$q_t = q_0 \exp^{-ri}$ $r_1 = \alpha_1 (t)$ $r_2 = \alpha_2 \mathrm{E(t)}$	t=time, E= fishing effort	Quinn (1987)
$q = 0.085\ N^{-0.384}$ $q = 0.287\ N^{-0.278}$	Haddock, George's Bank N = population abundance $Area$ = population habitat	Grecco and Overholtz (1990)
$q = 0.095\ N^{-0.787}$ $q = 0.003\ Area^{-0.747}$	Cod gill net, Atlantic B=Stock biomass $Area$ = population habitat	Rose and Legget (1991)
$q = q_1 \frac{T/q_2}{1+q_3 B_t}$	Peruvian anchoveta. q_1 = base fraction of the stock size per unit of effort (when stock size is low); B = biomass; T = temperature; q_2 and q_3 are constants	Hilborn and Walters (1992)
$q(\ell, t, E, F) = f(\text{size})$	ℓ = length, t = time, E = fishing effort; f = fleets	Arreguín-Sánchez (1996)

Materials and methods

We assume that catchability 1) is length dependent; 2) depends on fish behavior; 3) and is density dependent. For fishing effort, we also assume that 1) these assumptions can be valid for individual fishing fleets, such that we can explicitly consider the individual contribution of the several fleets participating in the fishing process and 2) that units of effort have static properties, that is to say, a consistent fishing power over time.

Length-dependent catchability

The catchability coefficient must be estimated for each length class in a given time, $q(\ell,t)$. A convenient form to represent the transformation of one length-frequency distribution (representing the structure of the stock) into another is by means of a transition matrix (Shepherd, 1987; Caswell, 1988), so that

$$N(\ell,t+1) = A(\ell,k)N(\ell,t), \qquad (2)$$

where k and ℓ = successive length intervals;
$N(\ell,t)$ = is the stock size in numbers at time t; and
A = the transition matrix that depends on growth and mortality.

Although these processes occur concurrently, Shepherd (1987) assumed that they can be separated as the product of two terms:

$$A(\ell,k) = G(\ell,k)S(k),$$

where G = the effect of growth in absence of mortality; and
S = the effect of mortality (survival) and also of selection of the sampling gear.

Matrix $G(\ell,k)$ can be easily estimated by following the criteria defined by Shepherd (1987) to assign growth probabilities to each length class. The elements of $S(k)$can be defined in terms of mortality as

$$S(k) = e^{-Z(k)t} = e^{-[M+q(k,t)s(k)E(t)]},$$

where $S(k)$ represents the values of the elements in the main diagonal of the survivorship matrix (other elements are zero; see Caswell, 1988); $Z(k)t$ is the instantaneous rate of total mortality for the k^{th} length group at time t; M is the instantaneous rate of natural mortality (assumed constant); $s(k)$ is the probability of gear selection for length k; and $E(t)$ is the fishing effort at time t (which is assumed nontargeted to specific sizes within a range of sizes captured by the gear). Then fishing mortality is given as $F(k, t) = q(k, t)\, s(k)E(t)$.

Equation 2 can therefore be represented as

$$N(\ell,t+1) = \sum_k G(\ell,k)e^{-[M+q(k,t)s(k)E(t)]}N(k,t). \qquad (3)$$

If $N(\ell\mathrm{t}+1)$, $N(k,t)$ and $G(\ell,k)$ are known, as well as M, $s(k)$, and $E(t)$, then $q(k,t)$ can be estimated. Equation 2 can then be solved iteratively for $q(k,t)$ by using an algorithm to minimize differences between observed and calculated values of $N(\ell, t+1)$.

Once $q(k,t)$ values are obtained, the catchability pattern with length can be observed and a tendency

quantified. Although a catchability-at-length model may be empirically determined, its interpretation must be made by considering the population biology and behavior of the fish. On an annual basis, the model is represented by the function

$$q(\ell)\alpha\beta(\ell)\cdot\ell \tag{4}$$

whose slope $\beta(\ell)$ represents the rate of change of catchability with length for a given year. If several years are considered for a stable period of the fishery, then a general function can be estimated where the slope of the length-based catchability pattern in Equation 4 can be expressed by $\beta(\ell,\bullet)$, where the symbol $\bullet$ represents the average stock level over a range of years in which it can be reasonably assumed to be stable.

Time-dependent catchability

Gulland (1983) expanded the scope of the catchability coefficient to a structured population as expressed in the following equation:

$$C(\ell,\Delta t) = q(\ell,\Delta t)s(\ell)E(\Delta t)N(\ell,\Delta t). \tag{5}$$

This represents the capture of fish of various sizes (ℓ) during a time period Dt. Taking the mean stock size ($\overline{N}$), and rewriting Equation 5 in terms of catch per unit of fishing effort, U, we obtain

$$U(\ell,\bullet) = q(\ell,\bullet)\overline{N}(\ell),$$

with $$U(\ell,\bullet) = C(\ell,\Delta t)/s(\ell)E(\Delta t)$$

and then

$$\begin{aligned}\mathrm{Ln}\left[U(\ell,t)/U(\ell,\bullet)\right] &= \mathrm{Ln}\left[q(\ell,t)\overline{N}(\ell)/q(\ell,\bullet)\overline{N}(\ell)\right]\\ &= \mathrm{Ln}\left[q(\ell,t)/q(\ell,\bullet)\right].\end{aligned} \tag{6}$$

This can be interpreted as the departure or anomaly in catchability at time t with respect to the average for a given length class. Arreguín-Sánchez (1996) suggested that this ratio is a linear function of size, represented by the midlength class as

$$\mathrm{Ln}\left[q(\ell,t)/q(\ell,\bullet)\right] = \alpha(t) + \beta(t)\ell, \tag{7}$$

where

$$\beta(t) = \mathrm{Ln}\left[q(\ell+1,t)/q(\ell,t)\right] - \mathrm{Ln}\left[q(\ell+1,\bullet)/q(\ell,\bullet)\right].$$

The intercept $\alpha(t)$ in Equation 7 can be interpreted as the relative vulnerability of small fish, and also as an index of the relative abundance of recruits. The slope $\beta(t)$ expresses the rate of change of catchability-at-length with respect to the average, or in other words, the departure (anomaly) from the average catchability pattern with length.

Once $\beta(\ell,\bullet)$ is estimated from Equation 4, the value of $\beta(t)$ can be added to $\beta(\ell,\bullet)$ to obtain the corresponding catchability values for a given time period.

Amount of fishing and density-dependent catchability

The relation between population size and catchability has been most studied in pelagic clupeoid fish (Murphy, 1966; MacCall, 1976; Csirke, 1988, 1989; Pitcher, 1996), where catchability is inversely related to stock size. Thus a density-dependent effect can be approached by considering the population as a whole, and the function

$$\overline{q}w(t) = f\{N(t)\} \tag{8}$$

can be fitted, where $\overline{q}w(t)$ is the weighted value of q at time t, with U at time t as a weighting factor. An analogous approach is proposed for each length class. For a stable period of time, we can assume that the amount of fishing, or the total fishing effort E, is one of the main sources of variation of the population density and the structure of the exploited stock. A change in both of these population characteristics will be reflected in the $\beta(t)$ coefficient. With Equations 1 and 8, it is possible to relate changes in $q(\ell,t)$ as a function of coefficient $\beta(t)$:

$$\beta(t)\alpha\,\beta(E)\cdot\ell, \tag{9}$$

where a constant natural mortality rate is assumed for all length classes over time.

Because $\beta(t)$ represents the departure of the catchability pattern with length at time t, Equation 9 measures the effect of the amount of fishing on the anomaly, and it is represented by the slope $\beta(E)$. The magnitude and sign of $\beta(E)$ will provide information about changes in stock density. A negative sign means that for a low level of fishing, q will increase with fish length.

Catchability differences between fleets

Following the same rationale as that in Equation 7, differences in q between fleets as a function of length can be estimated. If q and h represent two different fishing fleets, Equation 6 can now be expressed as

$$\mathrm{Ln}\left[U(g,\ell,t)/U(h,\ell,t)\right] = \mathrm{Ln}\left[q(g,\ell,t)/q(h,\ell,t)\right] \tag{10}$$

and

$$\mathrm{Ln}[q(g,\ell,t)/q(h,\ell,t)] = \alpha(f) + \beta(f)\cdot\ell, \qquad (11)$$

where f indexes fishing fleets.

In this case, the intercept $\alpha(f)$ is the relative difference in catchability between fleets for the smallest fish. The slope $\beta(f)$ reflects the difference in fishing performance measured as the anomaly in catchability of the fleet g with respect to the fleet h.

The additive catchability model

The deterministic model that incorporates the processes discussed can now be set out. It relies on the changes of the slope $\beta(\ell, \bullet)$, representing the catchability-at-length pattern, by the addition of the slopes of the partial effects described by Equations 7, 9, and 11. The slope of the catchability model, with the form defined by Equation 4, is represented by

$$\beta(\ell,t,E,f) = \beta(\ell,\bullet) + \beta(t) + \beta(E) + \beta(f). \qquad (12)$$

The value of $\beta(\ell, t, E, f)$ represents the slope of the catchability-at-length function without restriction to equilibrium, which has been compensated by the addition of the term $\beta(t)$, where t refers to any appropriate unit of time.

The red grouper (*Epinephelus morio*) fishery in the Campeche Bank, Mexico

The red grouper on the North continental shelf of Yucatan is exploited by three fleets: an artisanal and a mid-size fleet from Mexico, and a large-scale fleet from Cuba. These fleets overlap in respect to their fishing grounds (Moreno et al.[1]): Mexican fleets overlap in a range of 60% to 70%; the midsize fleet from Mexico and large-scale fleet from Cuban, around 60%; and the artisanal and Cuban fleets, between 12% and 16%. This overlap in fishing grounds means that each fleet causes fishing mortality on different sizes of the stock and thus necessitates that the fleets be considered separately for stock assessment purposes.

The artisanal fleet of Mexico is composed of vessels of approximately 9 m long, operating from the coast to 20 m depth, and catching mainly juvenile and preadult fish. The midsize fleet uses 15-m vessels operating at depths of 10 to 80 m, and catch comprises both juvenile and adult fish, according to the season. The Cuban fleet fishes mainly with 27-m vessels, operates between 20 and 90 m depth, and catches adult fish. Both Mexican fleets have free access and move seasonally in the area following changes in fish density (i.e. with reproductive aggregation). The Cuban fleet has a catch quota of 3900 t of demersal fish, of which more than 80% is red grouper. This fleet remains in the central and eastern region of the continental shelf of Yucatan most of the time.

Differences related to gear, fishing effort, and fishing strategies among fleets are described in Moreno (1980), Burgos (1987), and Fuentes (1987) for the midsize fleet; Sáenz et al. (1987), Salazar (1988), and Solana-Sansores and Arreguín-Sánchez (1991) for the artisanal fleet; Valdés and Padrón (1980) for the Cuban fleet; and Seijo (1986), González-Cano et al. (1993), and Arreguín-Sánchez et al. (1996) for the three fleets. In this paper we used standardized fishing days as the unit of fishing effort.

For the catchability model, available data for the red grouper fishery are summarized in Table 2. Detailed information is derived from the midsize fleet, which harvests around 70% of the total annual yield. Other fleets share the remaining 30% more or less equally. Because the midsize fleet also catches a size range that overlaps the other two, this fleet is the start of our analysis. Later, we will incorporate the other fleets into the catchability model.

To solve Equation 3, we assumed that individual growth follows the von Bertalanffy equation with values of L_∞ = 87 cm total length (TL) and K = 0.12/year (Arreguín-Sánchez[2]), and the natural mortality coefficient M = 0.3/year (Doi et al., 1981; Contreras et al., 1994).

The selection factor for each length class $s(\ell)$, representing a probability term directly affecting the abundance of length classes in the catch, was set to be $s(\ell)$ = 1. For simplicity, red grouper fishery gears were assumed nonselective (hook-and-line and hand lines with different sizes and baits).

Annual catch-per-unit-of-effort(U)-at-length data for the period 1973 to 1987 for the midsize fleet was used. The iterative procedure described for Equation 3 was applied to each pair of yearly data to obtain initial values of catchability per length class and year. Catchability values for each length class $q(\ell, y)$ were used to fit the trend with length (Fig. 1) and to describe variability of $q(\ell,\bullet)$. The solution for Equation 3 does not require a previous knowledge of recruits at $U(\ell, t)$ and $U(\ell, t+1)$, and it was solved for

[1] Moreno, V., F. Arreguín-Sánchez, M. Contreras, and R. Burgos. 1991. Analysis of usage patterns in shared stocks: the red grouper fishery from the continental shelf of Yucatan, Mexico. Proc. 44th Ann. Sess. Gulf and Caribb. Fish. Inst., 18 p. [Mimeo.]

[2] Arreguín-Sánchez, F. 1996. Length-based growth estimation for the red grouper (*Epinephelus morio*) in the North continental shelf of Yucatan, Mexico. Centr. Interdiscip. Cienc. Mar., México, 19 p. [Manuscript.]

Table 2

Summary of the data used in this paper for the red grouper fishery on the north continental shelf of Yucatan, Mexico. Fleets operate with long lines of different sizes (artisanal also uses hook-and-line). Fishing effort was standardized as fishing days (see Arreguín-Sánchez et al., 1996)

Fleet	Annual catch-at-length	Monthly catch-at-length	Sampling design	Site of landing
Artisanal[1]	1987	1987	three stages (port, vessels, baskets)	Ports along the coast of Yucatan, Mexico
Midsize[2]	1975 to 1987 (except for 1986)	1975 to 1987 (except for 1986)	two stages (day/vessel and commercial size)	Port of Progreso, Mexico
Cuban fleet[2]	1975 to 1987		two stages (vessels and commercial size).	Port of La Havana, Cuba

[1] Source: Centro de Investigación y de Estudios Avanzados del IPN, Yucatan, Mexico.
[2] Source: Instituto Nacional de la Pesca. Centro Regional de Investigación. Pesquera de Yucalpetén, Yucatan, Mexico.

$n-1$ or $n-2$ catchability values, with differences in n caused by the absence of recruitment estimates. Because we fitted the general tendency as a catchability-at-length pattern, one or two missing points will not affect the estimates.

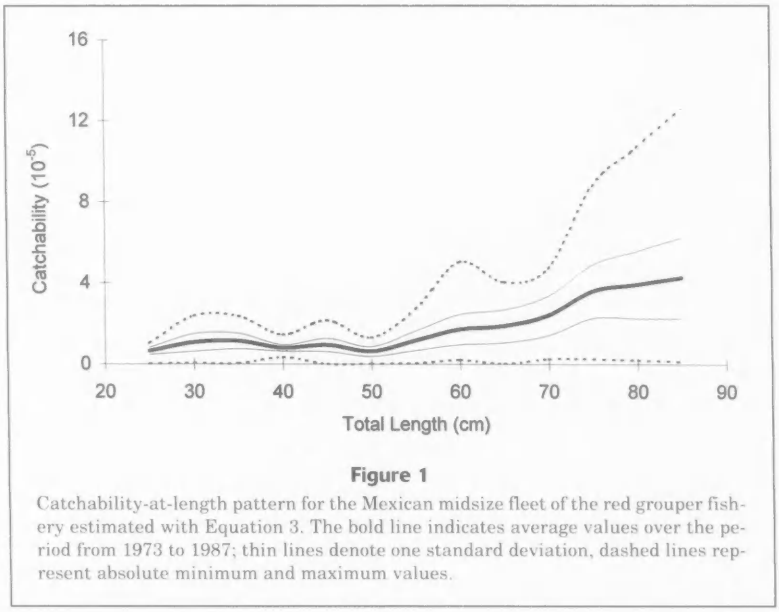

Figure 1

Catchability-at-length pattern for the Mexican midsize fleet of the red grouper fishery estimated with Equation 3. The bold line indicates average values over the period from 1973 to 1987; thin lines denote one standard deviation, dashed lines represent absolute minimum and maximum values.

Results

Length-dependent catchability

The fitting process required some consideration of population behavior because trend could be adjusted to an exponential or sigmoidal function. We decided on a sigmoidal form because of reproductive behavior. During reproductive aggregation, adult fish (>50 cm TL) form groups with a sex ratio (females: males) close to 6:1, comprising individuals of around the same size, but without any apparent size segregation between groups. This is well known by fishermen, and has been described by Moe (1969), Shapiro (1987), and Mexicano-Cíntora (1990). In terms of fishing, adults within a specific area have the same probability of catch. In the catchability-at-length trajectory, we think this reproductive behavior can be well represented by an asymptotic trend of catchability for large fish.

The variation in catchability of young fish, as expressed by one standard deviation (Fig. 1) was similar for lengths between 20 to 50 cm and increased sharply after first maturity (at 50 cm TL, as defined by Mexicano-Cíntora, 1990).

The generalized catchability-at-length equation fitted for the red grouper was

$$q(\ell,\bullet) = \frac{0.00004256}{1+e^{-[3.896+0.0064\cdot\ell]}} \qquad (13)$$

with the standard error (SE) of the ordinate $SE\alpha$ = 0.773, and SE_β = 0.012 for the slope; R^2 = 0.728 (df=10).

Time-dependent catchability

Time variation of catchability was analyzed considering both annual and monthly catch-structured data. From Equation 7, parameters $\alpha(y)$ and $\beta(y)$ were estimated by regressing

$$\mathrm{Ln}[U(\ell,t)/U(\ell,\bullet)]$$

with length (Fig. 2). Table 3 shows values of the constants for both midsize Mexican and Cuban fleets for annual data.

On a monthly basis, the same computations were developed for the mid-size fleet. Departures represented in parameters $\alpha(m)$ and $\beta(m)$ were estimated in a similar way to those in Equation 7, but considering annual catch-structured data. Seasonal changes in vulnerability occurred: q increased in winter (December to February) in synchrony with the reproductive aggregation (Fig. 3). Catchability was lower in autumn, when the population is dispersed along the continental shelf and the vulnerability of young fish in coastal waters increases.

Catchability differences between fleets

Following Equation 11, differences between fleets were evaluated by comparing annual data for the Cuban fleet with those of the midsize fleet for the period 1975 to 1987. Mexican mid-size and artisanal fleets were compared on a monthly basis for 1987. Parameters for $\alpha(f)$ and $\beta(f)$ were obtained (Tables 4 and 5). Positive values of $\beta(f)$ indicate that relative catchability for small fish is higher for the midsize fleet than for the Cuban fleet; and lower for large fish. This scheme represents differences in fishing areas between fleets. The negative value $\beta(f)$ for in 1982 suggests fleets changed their usual behavior. Similar interpretation can be made for monthly data between the artisanal and midsize fleets.

Figure 3 shows the tendency of

$$\mathrm{Ln}[U(\text{mid-scale},\ell,t)/U(\text{Cuban},\ell,t)]$$

with length. An inflection point is observed just at the length at first maturity (i.e. 50 cm LT). Positive values indicate that q is higher in small (immature) fish for the midsize fleet than for the Cuban fleet, whereas q is equal in both fleets for mature fish. For the tendency of

$$\mathrm{Ln}[U(\text{artisanal},\ell,t)/U(\text{mid-scale},\ell,t)]$$

with length, catchability of immature fish was higher for the artisanal than for the midsize fleet, and again equal for adult fish up to 65 cm TL. For fish larger than 65 cm, q was higher in the midsize fleet.

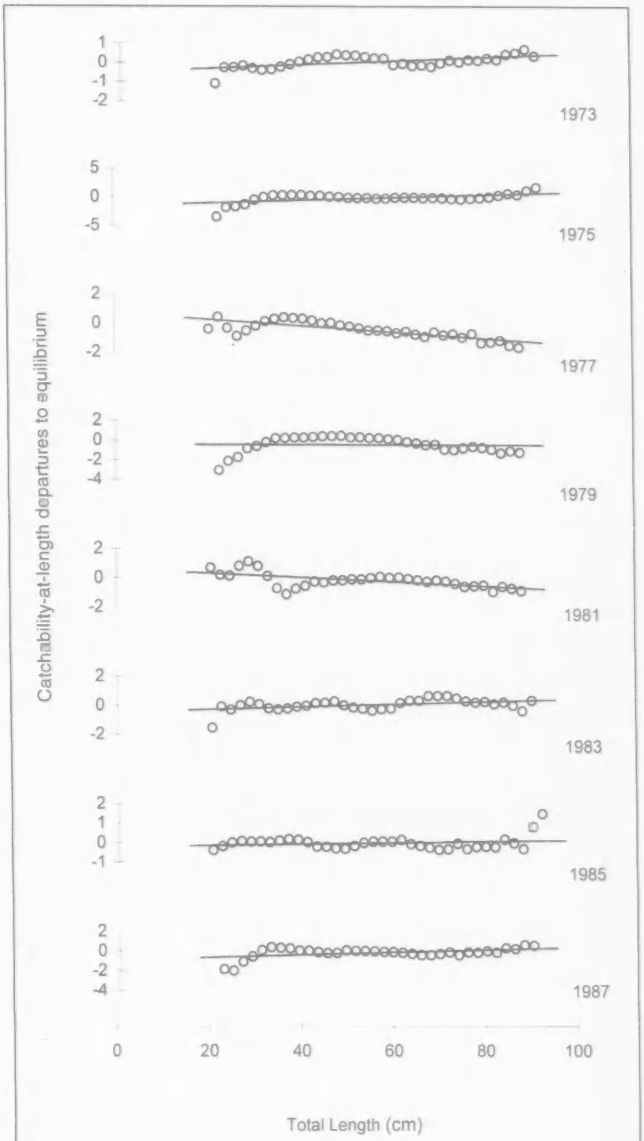

Figure 2

Annual tendencies of the ratio $\mathrm{Ln}[U(\ell,t)/U(\ell,\bullet)]$ with length for the Mexican midsize fleet of the red grouper fishery representing departure of catchability-at-length pattern with respect to equilibrium, as expressed in Equation 6.

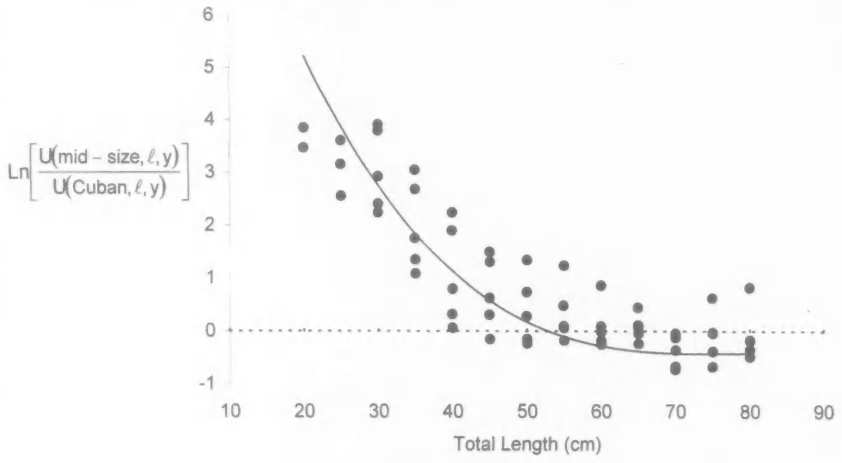

Figure 3

Trend in catchability-at-length differences, between Mexican midsize and Cuban fleets for the period 1975 to 1979, as expressed by Equation 11. Positive values indicate higher vulnerability for immature fish for the midsize fleet than for the Cuban fleet. Vulnerability of adult fish to both fleets is equal.

Table 3

Parameters of Equation 7 for the Mexican midsize and Cuban fleets for the red grouper fishery. $\alpha(y)$ expresses relative vulnerability of recruits each year and $\beta(y)$ departure of catchability trend with length, both with respect to equilibrium. (*P<0.05; **P<0.01).

Year	$\alpha(y)$ midsize	$\beta(y)$ midsize	R^2	$\alpha(y)$ Cuban	$\beta(y)$ Cuban	R^2
1973	–0.509	0.010	0.405*			
1974	0.508	–0.013	0.664*			
1975	0.511	–0.010	0.487**	–1.494	–0.018	0.602*
1976	0.953	–0.025	0.610**	0.865	–0.006	0.507**
1977	0.683	–0.022	0.600**	0.767	0.024	0.624*
1978	1.045	–0.024	0.686**	0.416	0.047	0.496*
1979	0.941	–0.021	0.757*	–1.396	0.033	0.771**
1980	–0.612	0.015	0.614**	–2.925	–0.043	0.544**
1981	0.476	–0.013	0.643**	–2.147	–0.026	0.622*
1982	0.487	–0.012	0.396*	1.923	–0.021	0.483**
1983	–0.401	0.009	0.371*	1.448	0.020	0.701**
1984	0.175	–0.005	0.446**	0.828	0.079	0.513**
1985	0.135	–0.004	0.432*	–1.126	0.026	0.661**
1986	–1.064	0.023	0.739*	–4.889	0.079	0.596**
1987	–0.915	0.013	0.581*	–1.250	0.026	0.470**

Amount of fishing and density-dependent catchability

As in Equation 9, values of $\beta(y)$ from Table 3 were fitted against fishing effort at time t. Figure 4 shows the tendency for both the midsize and Cuban fleets. For the midsize fleet, the model gives the following values for the parameters: $\alpha(E) = 0.1252$, $\beta(E) = 4.8 \cdot 10^{-6}$; $R^2 = 0.74$. Although the tendency for the Cuban fleet was also negative, the observed variability was

higher, and at least two probable tendencies were empirically identified (Fig. 4B), both of them as a consequence of changes in the catch quota assigned to the Cuban fleet. For further computations, the density-dependent effect was assumed to be similar for both fleets because of the absence of more detailed information to support quantitative analysis. This assumption is reasonable because both fleets average more than 60% overlap in a year, but almost 100% during reproductive aggregation.

Because of the evident differences in behavior between juvenile and reproductive fish, the density-dependent effect of the amount of fishing was also applied within each length class, as in Equation 9. Parameters of the model are given in Table 6. Variation of the slope $\beta(E)$ with length class is shown in Figure 5. Once again, immature fish behaved differently from adults. The density-dependent effects for immature fish were constant, whereas the same effect increased with size for sizes >50 cm TL. It is clear that the density-dependent effect during aggregation promotes a greater catchability, and because the older adult fish tend to remain longer in deeper waters (Shapiro, 1987), the density-dependent effect will increase with size (age).

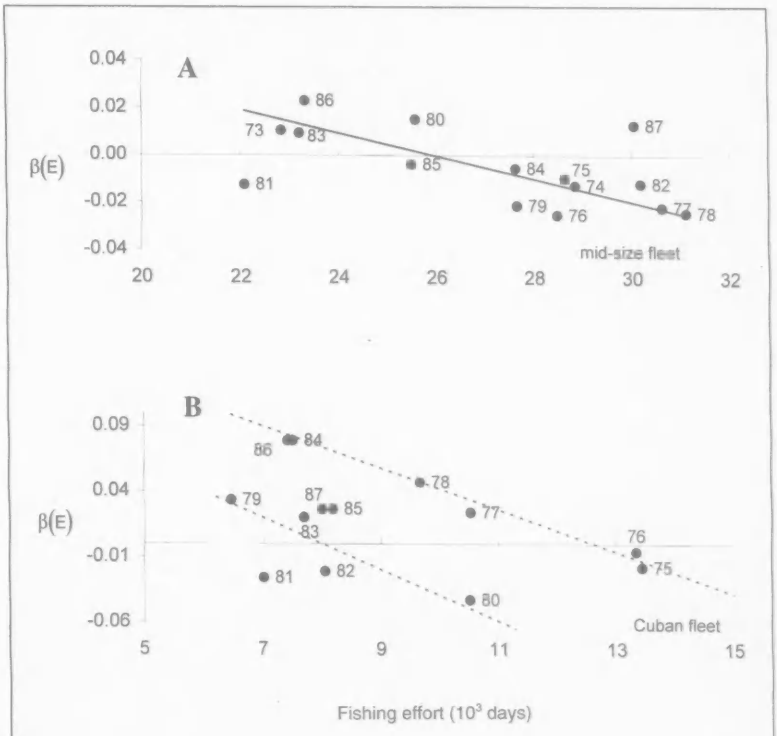

Figure 4

Estimation of density-dependent effects on catchability-at-length pattern for (**A**) the Mexican midsize fleet and (**B**) Cuban fleet of the red grouper fishery (Eq. 11). General trends suggest density-dependent effects by fleets are of the same magnitude (see text for interpretation).

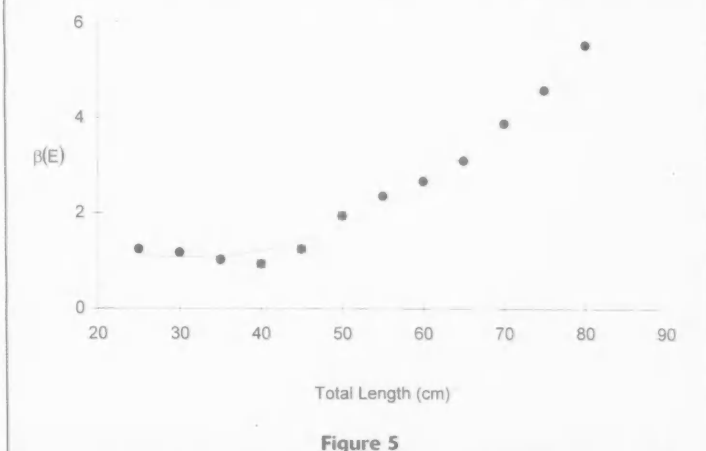

Figure 5

Trend in density-dependent effects on q within each length class with size.

The additive catchability model for the red grouper fishery

Once several sources of variation were estimated, a model (Eq. 12) was obtained by adding partial effects to the slope of Equation 13, as follows:

$$q(\ell,t,f,E) = \frac{0.00004256}{1+e^{-\left\{3.896+\beta(\ell,y,m)(f,E)\right\}}},$$

where

Table 4

Estimates of parameters for Equation 11 describing departure of catchability coefficient with length for the Cuban fleet with respect to the Mexican midsize fleet for the red grouper fishery (*P<0.05; **P<0.01).

Year	$\alpha(f)$	$\beta(f)$	R^2	n
1975	–4.474	0.052	0.636**	14
1976	–2.956	0.047	0.613*	13
1977	–3.590	0.058	0.807**	14
1978	–3.904	0.065	0.822*	12
1979	–5.186	0.076	0.795*	11
1980	–4.713	0.055	0.736*	12
1981	–6.476	0.097	0.708*	13
1982	0.323	–0.020	0.711**	9
1983	–4.527	0.051	0.713*	10
1984	–3.936	0.059	0.561**	11
1985	–3.847	0.050	0.848**	13
1986	–6.149	0.070	0.873*	13
1987	–3.942	0.055	0.606*	11

Table 5

Estimates of parameters for Equation 11 describing departure of catchability coefficient with length for the midsize fleet with respect to the artisanal fleet, both from Mexico (*P<0.05; **P<0.01).

Month	$\alpha(f)$	$\beta(f)$	R^2	n
January	2.953	–0.071	0.576*	23
February	2.654	–0.083	0.701**	22
March	4.180	–0.107	0.719*	24
April	7.904	–0.230	0.965**	14
May	2.524	–0.064	0.769*	28
June	1.295	–0.032	0.483*	31
July	1.426	–0.041	0.720*	28
August	–1.589	0.041	0.562**	16

Table 6

Estimates of parameters for Equation 9 representing density-dependent effects within each length class (n=13, df=11; *P<0.05; **P<0.01).

Total length (cm)	$\alpha(E)$ 10^{-8}	Standard error $\alpha(E)10^{-7}$	β(E) 10^{-8}	Standard error β(E)10^{-9}	R^2
25	3.76	1.211	1.238	1.282	0.89**
30	31.05	3.356	1.164	3.471	0.50**
35	54.72	3.276	1.013	2.905	0.52**
40	48.32	1.574	0.926	2.013	0.66*
45	26.39	1.147	1.237	2.718	0.65*
50	3.68	1.091	1.936	2.426	0.85*
55	–0.31	1.123	2.360	2.974	0.85*
60	0.62	1.144	2.678	2.857	0.89*
65	1.56	1.316	3.198	1.892	0.96**
70	–1.17	1.388	3.886	2.593	0.95**
75	–2.83	1.510	4.589	2.621	0.96**
80	0.43	0.743	5,549	3.282	0.96*

$$\beta(\ell,y,m,f,E) = \beta(\ell,\bullet) + [\beta(y),\beta(m)] + \beta(f) + \beta(E),$$

where i indexes fleet, and each constant takes the corresponding value, depending on the specific length class (ℓ), time, year (y) or month (m), fleet (f), and the specific density-dependent effect (E).

Discussion

The catchability model incorporates several sources of variation, such as individual size, time variations, and density-dependent effects, for which we assumed fishing effort is the most important variable affecting fish density, and the participation of several fishing fleets which differ in gear, catching power, and effort allocation.

The additive-catchability model, as applied to the red grouper, performed well and allows us to identify some aspects of fish behavior that influence catchability. For example, reproductive aggregation increases vulnerability of fish. Of particular importance are the relative constancy of catchability and its variance for immature individuals, and the increasing vulnerability of adult fish with size, especially during reproductive aggregation. This is related to the reproductive behavior of the population. Young fish remain close to the coast, with east–west seasonal displacements, whereas adults move across the continental shelf and aggregate during winter for reproduction. This means that juveniles and adults respond differently to fleets. The model also identified the differential accessibility of specific size ranges to different fleets. This is important because, in a fully exploited fish resource such as the red grouper, controls on fishing mortality must enhance survival of spawners and recruits. Figure 6 summarizes the relation between fishing effort, maturity, and seasonal changes in catchability for the red grouper fishery. During reproductive aggregation, identified by the maturity index, vulnerability increases and vessels spend less fishing effort to obtain a given level of yields. After reproduction, groupers disperse along the continental shelf and fleets must increase fish-

ing intensity because vulnerability of fish will decrease.

For the density-dependent catchability, the model describes fish behavior reasonably well. The red grouper is a gregarious and territorial fish. Stock density is reflected straightforwardly in yields. If fish densities decrease, q will decrease, and vice versa. This response to the amount of fishing is reflected by the model.

For the catchability model, note that although a transition matrix is very helpful for the estimation process, the form of the catchability-at-length function must be interpreted with good understanding of the biology of the exploited fish resource and of the fishery. Fish biology probably is the most important aspect because the effect of other sources of variation are added to the slope of this function.

The resulting catchability model can be easily incorporated into estimations of fishing mortality and population size; i.e. for the mid-size fleet at time t, fishing mortality can be expressed by

$$F(\ell,t,\text{midsize},E) = q(\ell,t,\text{midsize},E)\cdot E(t,\text{midsize}). \quad (14)$$

For the population size, the participation of the three fleets can be incorporated,

$$N\left(\ell,t,\sum_{i=1}^{3} f_i,E\right) = \frac{F\left(\ell,t,\sum_{i=1}^{3} f_i,E\right)C\left(\ell,t,\sum_{i=1}^{3} f_i\right)}{F\left(\ell,t,\sum_{i=1}^{3} f_i,E\right)\left[1-e^{-\left[M+F\left(\ell,t,\sum_{i=1}^{3} f_i,E\right)\right]}\right]}. \quad (15)$$

Despite the potential use of the catchability coefficient in some stock assessment models (i.e. age-based virtual population analysis, VPA, Pope, 1972; and length-based VPA, Jones 1981, 1984; Gulland[3]), Equations 14 and 15 suggest an alternative stock assessment tool, based on length-composition data.

A detailed description of catchability through the additive model reflecting fish behavior and fishery practices could be very useful for management purposes when it is incorporated into assessment models such as the above. Currently the red grouper fishery is subjected to heavy fishing where the main problems are intensive fishing of juveniles and the high vulnerability of adults. Because the additive catchability model describes these processes and incorporates all fleets, results can strongly aid management decisions based on a differential control of fishing mortality within the stock structure and between fleets.

Even when the model can describe the study well, we observed some critical aspects during application. The first is that we must know red grouper behavior sufficiently well to decide the form of the catchability-at-length relation (Eq. 4). Statistical criteria (i.e. a correlation coefficient) are not sufficient. A wrong interpretation of this could mean a disaster for the fishery. A second and similar aspect can occur for density-dependent catchability. The third aspect is the significance of sources of variation. Because the catchability model is based on the addition of the slopes of each particular variable and relation (i.e. with length, time, etc.), we must test that these slopes are significantly different from zero (see Equations 4, 7, 9, and 11), and if they are not different, the source of variation tested does not help to explain changes in q.

The fourth aspect involves the number of parameters to be estimated, which usually is taken as proportional to the complexity of the model computations, and inversely related to applicability. For the present case, the number of parameters in the model is $n + 2$, where n is the number of sources of varia-

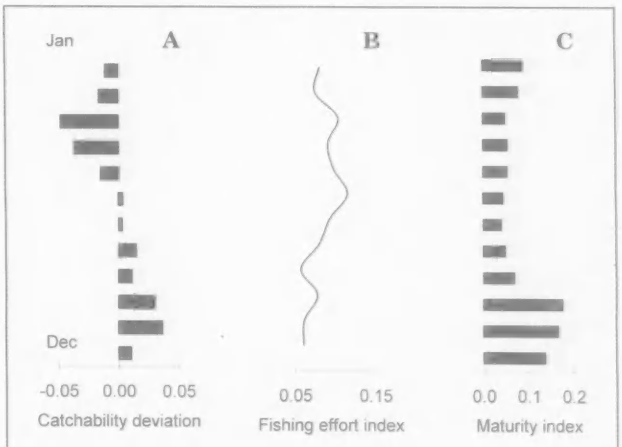

Figure 6

Schematic representation of the main q features of the red grouper fishery on the Campeche Bank: (**A**) seasonal catchability variation represented as departure of the annual average; (**B**) fishing effort index, represented as a monthly proportion of the year; (**C**) maturity index, reflecting diameter of oocytes.

[3] Gulland, J. A. 1965. Estimation of mortality rates. Annex to rep. Arctic Fish. Working Group. ICES Council Meeting (CM), 1965, paper 3, 9 p.

tion to be considered. However, the number of constants to be estimated strongly increases with the length of the time-series of data as $3(m \bullet y \bullet f) + 2(\ell) + 2$, with m = number of months, y = number of years, f = number of fleets, and ℓ = number of length classes. For example, in our study case, with $y = 13$, $f = 2$, and $\ell = 12$, the number of constants to be estimated will be 104. We think these are a lot of parameters; however, they are easily estimated because all of them are obtained by regression or by an analogous technique.

Acknowledgments

Some of the initial ideas developed in this paper were inspired by the late John A. Gulland, while F. A.-S. was at the Renewable Resources Assessment Group, London, in 1989. We want to dedicate this contribution to his memory. Our gratitude is also extended to S. Rodríguez, L. Capurro, and D. Pauly for their support and valuable comments on an early draft. We also thank three anonymous referees for their valuable comments. The first author was funded by the National Polytechnic Institute through COFAA, EDD and DEPI. Lastly, we thank Ellis Glazier, CIBNOR, who edited the English-language text.

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Foraging habits of bluefish, *Pomatomus saltatrix*, on the U.S. east coast continental shelf*

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Abstract.—After spending summer months in estuaries, spring- and summer-spawned young-of-the-year (YOY) bluefish, *Pomatomus saltatrix*, migrate out to continental shelf waters of the Mid-Atlantic Bight in early autumn. Adult bluefish are found on the continental shelf throughout summer and fall. Both juveniles and adults have high food consumption rates and are generally piscivorous. To determine principal prey types on the shelf, dietary analyses were performed on YOY and adult bluefish collected from National Marine Fisheries Service autumn bottom trawl surveys in 1994 and 1995. Both spring- and summer-spawned YOY bluefish diets were dominated by bay anchovy. However, the significantly larger size of the spring-spawned cohort was associated with the consumption of other prey species such as squid, butterfish, striped anchovy, and round herring. Summer-spawned bluefish were significantly smaller in 1995 than in 1994; diet and prey size comparisons suggest that body size had a dramatic influence on the amount of piscivorous feeding in the summer-spawned cohort. Adult bluefish diet was dominated by schooling species such as squid, butterfish, and clupeids. Cannibalism was virtually nonexistent. Daily ration estimates of YOY bluefish on the shelf (4–12% body wt/d) were similar to estuarine estimates in late summer. It is estimated that during the month of September, YOY bluefish in aggregate consumed 6.0 to 6.8 billion bay anchovies in 1994 and from 2.2 to 5.3 billion in 1995. The effect of this predatory loss on population dynamics of bay anchovy and the fish community on the continental shelf is unknown.

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One of the dominant marine piscivores along the U.S. east coast is the bluefish, *Pomatomus saltatrix* (Juanes et al., 1996). Bluefish spawned in offshore waters of the South Atlantic Bight in the spring (spring-spawned) are advected northward in waters associated with the Gulf Stream (Hare and Cowen, 1996) and move into mid-Atlantic Bight estuaries in June at ~60 mm fork length (Kendall and Walford, 1979; Nyman and Conover, 1988; McBride and Conover, 1991). A second wave of recruits consisting of summer-spawned fish occur in nearshore waters from mid to late summer.

In estuaries, bluefish exhibit rapid growth rates that are fueled by high food consumption and evacuation rates (Juanes and Conover, 1994; Buckel et al., 1995; Buckel and Conover, 1996). In the Hudson River estuary, for example, predation by bluefish is high enough to account for virtually all natural mortality of young-of-the-year (YOY) striped bass during their summer–fall growing season (Buckel et al., 1999). After spending the summer months in estuaries, YOY bluefish migrate back out onto the shelf and migrate southward to overwinter (Munch and Conover, in press). Spring-spawned YOY bluefish migrate out of estuaries at a size of ~180 mm fork length (FL) and ~100 g (Nyman and Conover, 1988; McBride and Conover 1991). By age 1, these spring-spawned fish attain sizes of ~260 mm FL and weights of ~300 g (Chiarella and Conover, 1990). Therefore, an individual spring-spawned bluefish gains from 100 to 200 g during its autumn migration. Given a 15% gross growth efficiency (Juanes and Conover, 1994; Buckel et al. 1995), a single bluefish could thus consume from ~650 to 1300 g of prey.

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Compared with the nearshore phase of the early life history of bluefish, our knowledge of the foraging ecology and predatory impact of bluefish on the continental shelf is poor. Here we quantify the diet of YOY and adult bluefish and determine YOY bluefish prey type and size selectivity patterns, foraging chronology, daily ration, and biomass of prey consumed during the autumn migration on the shelf.

Methods

Study area and collections

YOY and adult bluefish and their potential prey were collected on the U.S. east coast continental shelf during the autumn of 1994 and 1995 aboard the research vessel *Albatross IV*. Collections were made during the National Marine Fisheries Service, Northeast Fisheries Science Center's (NMFS-NEFSC) autumn bottom trawl survey cruises at predetermined stations from Cape Hatteras, NC, to Nova Scotia. Cruises began in early September and ended in late October in both years (6 September to 28 October 1994 and 5 September to 27 October 1995).

Descriptions of the survey design and the trawl characteristics can be found in Azarovitz (1981). Briefly, tows were made with a no. 36 Yankee trawl equipped with rollers with an opening 3.2 m high, 10.4 m wide, with 12.7-cm stretched mesh in the opening, with 11.4-cm stretched mesh in the codend, and with a 1.25-cm stretched mesh lining in the codend and upper belly to retain YOY fishes. Tows were 30 minutes in duration at 3.5 knots in relation to bottom and were conducted on a 24-h basis.

Dietary analyses

Adult and YOY bluefish were distinguished by using length-age relationships. Munch and Conover (in press) examined the annual size distributions of bluefish from autumn bottom trawl surveys conducted since the 1970s in four different regions of the shelf: SOC=South of Chesapeake Bay; C–D=Chesapeake Bay to Delaware Bay; SNE=Southern New England (Delaware Bay to Narragansett Bay); and Georges Bank. On the basis of these size distributions and backcalculated sizes at age 1 (Chiarella and Conover, 1990, and references therein), they classified YOY bluefish in autumn as those fish ≤300 mm FL. We classified adults as those bluefish >300 mm FL and we distinguished spring- and summer-spawned YOY bluefish for each region in 1994 and 1995 on the basis of bimodality in length-frequency distributions (Munch and Conover, in press). We also adopted Munch and Conover's (in press) geographical boundaries for this analysis. In 1994, summer-spawned bluefish sizes by region were as follows: SOC, FL≤120 mm; C–D, FL≤160 mm; and SNE, FL≤160 mm. In 1995, summer-spawned bluefish sizes were as follows: SOC, FL≤100 mm; C–D, FL≤150 mm; and SNE, FL≤140 mm. Spring-spawned bluefish were those fish larger than the summer-spawned cohort by region but ≤300 mm FL.

Diets of spring- and summer-spawned juveniles and adult bluefish were quantified. Bluefish taken for stomach content analysis were wet weighed (±1.0 g) and measured for fork length, FL (to 1.0 mm). Stomachs were removed at sea and preserved in 10% formalin buffered with sea water. On some occasions, whole fish were either frozen or preserved in 10% formalin and then processed in the laboratory. Stomach contents of bluefish were identified to the lowest possible taxon, enumerated, blotted dry, weighed (±0.01 g), and measured (TL for fish prey and mantle length for squid, ±1.0 mm). Eye diameter (±0.1 mm) and caudal peduncle height (±0.1 mm) were measured for partially eaten bay anchovy and butterfish prey and converted into TL from linear regression equations (Scharf et al., 1997; Scharf et al., 1998a).

Each trawl containing bluefish provided us with a group or "cluster" of bluefish for a given station. Therefore, for our analysis, the mean and variance of diet indices were calculated with cluster sampling estimators developed at the NEFSC-NMFS, Woods Hole, MA (Cochran, 1977, Fogarty, unpubl. data). These calculations are described in a previous study that examined bluefish diet in the Hudson River estuary (Buckel et al., 1999).

Net feeding

During a 30-minute tow, bluefish may feed within the trawl (an activity known as net feeding). Net feeding could bias the diet index estimates or affect gut fullness level estimates (or do both). We tested for such bias by classifying fish or squid prey as either 1) "fresh" or 2) "digested" during our stomach content examination. "Fresh" prey had no sign of digestion and "digested" prey were either partially or well digested (e.g. they were anywhere from starting to lose skin to being only identifiable by skeleton or shape). The percent occurrence of four dominant prey (bay anchovy, striped anchovy, butterfish, and squid) were compared between fresh and digested categories in YOY bluefish. If the percent occurrence of each prey category within a cohort and region was similar for fresh and digested prey, it would suggest that either there was no net feeding or that it did not affect diet index estimates.

Prey-type selectivity

The feeding selectivity of spring-spawned bluefish on the continental shelf was determined from the relative abundance of prey in individual bluefish guts and the relative abundance of prey in trawl catches. Four prey categories were examined in 1994 (bay anchovy, butterfish, squid, and "other") and three prey categories in 1995 (bay anchovy, squid, and "other"). The "other" category included any teleost fish that did not fall into the previously mentioned groups. The relative abundance of these prey in the field was calculated by including only those prey that were of a size that bluefish could theoretically consume (prey FL<80% of bluefish FL; determined from an independent study, Scharf et al., 1997). Additionally, the index was calculated for stations where at least ten spring-spawned bluefish were captured. Chesson's (1978) index was used to determine bluefish prey preference as

$$\alpha_i = \frac{r_i / p_i}{\sum_{j=1}^{m} r_j / p_j}, \qquad i = 1,\ldots\ldots,m,$$

where α_i = the selectivity for prey type i for an individual bluefish;
r_i = the relative abundance of prey type i in an individual bluefish stomach;
p_i = the relative abundance of prey type i in the environment; and
m = the number of prey types available.

Values of α_i were averaged for each year. Random feeding occurs when mean $\alpha_i = 1/m$ (1994=0.25 and 1995=0.33); values of $\alpha_i > 1/m$ or $\alpha_i < 1/m$ represent "selection" and "avoidance" of prey, respectively. Random feeding was tested by using a t-test to compare mean α_i with $1/m$ for each prey type within each year (Chesson, 1983).

Prey-size relationships and size selectivities

Prey sizes of all bluefish prey were measured directly or determined indirectly from regression equations. The relationship between ingested prey size and bluefish length was determined for YOY and adult bluefish in both 1994 and 1995. In order to compare the relative prey size ingested by spring- and summer-spawned bluefish cohorts in 1994 and 1995, the frequency distributions of bay anchovy FL to bluefish FL ratios were examined. Ratios were calculated for all bay anchovy prey that were measured (1994, n=388; 1995, n=202).

Size-selective feeding on bay anchovy prey was examined by comparing the sizes of bay anchovy ingested by bluefish at a specific station with sizes of bay anchovy captured in the trawl at that station. Stations from 1994 and 1995 that had n>15 bay anchovy length measurements for each bluefish cohort were used in the analysis. Bay anchovy lengths at each station were obtained from archived data at NEFSC-NMFS, Woods Hole, MA.

Selectivity for bay anchovy prey size categories was measured by using Chesson's (1978) index (described above). Bay anchovy lengths ingested by bluefish and collected at each station were partitioned into four bay anchovy FL categories: 25–34, 35–44, 45–54, and 55–64 mm. Values of α_i were calculated from individual bluefish for each size bin at each station separately; these were then averaged across stations. As above, values of $\alpha_i > 1/m$ or $\alpha_i < 1/m$ represent "selection" and "avoidance" of size categories, respectively. Estimated values of mean α_i were compared with $1/m$ by using a t-test (1994 spring-spawned, $1/m$=0.25, and summer-spawned, $1/m$=0.33; 1995 spring-spawned, $1/m$=0.33).

Feeding chronology, daily ration estimates, and impacts on bay anchovy

Values of gut fullness were used to examine feeding chronology of YOY bluefish. Gut fullness values (F) were calculated as

$$F = G / W,$$

where G = prey wet weight; and
W = bluefish wet weight (total weight minus prey wet weight).

Gut fullness values for individual bluefish were pooled over eight 3-h time periods and averaged. This analysis was performed for both spring- and summer-spawned bluefish by geographic region.

In order to estimate feeding rates of bluefish on the shelf, bluefish gastric evacuation rate (GER) estimates were needed. Previous work on YOY bluefish GER showed that prey type and bluefish body size did not have a significant effect on bluefish GER; of the factors examined, temperature had the only significant effect on bluefish GER (Buckel and Conover, 1996). These laboratory experiments described bluefish GER from 21° to 30°C. In our continental shelf collections, YOY bluefish were found in water temperatures as low as 15°C (mean of surface and bottom temperature). Therefore, a laboratory experiment to measure YOY bluefish GER at 15°C was performed.

The experiment was conducted in an identical manner to previous GER experiments on YOY blue-

fish (Buckel and Conover, 1996). Briefly, YOY bluefish were acclimated to experimental tanks for two weeks, acclimated to 15°C for 3 days, and then held at 15°C for a 12–48 h starvation period. They were then fed a single meal of previously frozen and thawed adult bay anchovy (bluefish sizes were: mean bluefish TL=122 [range=99–146], mean wet weight=15.79 g, prey mean wet weight=0.88 g, mean prey wt/predator wt=5.8%). After a predetermined period of time, individual bluefish were sacrificed and their stomach contents removed, blotted dry, and weighed (±0.01 g).

The exponential GER model (see Buckel and Conover, 1996) was fitted to the proportion of meal remaining versus time by using nonlinear regression analysis. The GER estimate from this experiment was used along with estimates from Buckel and Conover (1996) to develop an empirical function describing YOY bluefish GER from 15° to 30°C. This function was used to estimate bluefish GER from water temperatures at which bluefish were collected on the continental shelf. Bluefish daily ration was estimated for each cohort by region in 1994 and 1995 with the Eggers (1979) equation:

$$D = \overline{F}_i \cdot R_e \cdot 24,$$

where D = is bluefish daily ration;
$\overline{F}_i$ = the mean gut fullness over 24 hour; and
R_e = the exponential gastric evacuation rate (see above).

Mean gut fullness was calculated by taking the average of the individual time period (i) gut fullness means from the feeding chronology analysis (see above). The mean of the means was used to give each time period equal weight even though sample sizes for given time intervals varied over the diel cycle. Daily ration was calculated for those geographical regions and cohorts that had a sufficient diel record (e.g. gut fullness estimates throughout the diel cycle). The standard error of the daily ration estimate was approximated by using the delta method (Seber, 1973).

Estimates of the biomass of prey consumed by the YOY bluefish population during their southward migration requires estimates of the numbers of YOY bluefish in the population. The NEFSC, NMFS, Woods Hole, MA, has used virtual population analysis (VPA) to estimate the abundance of the east coast bluefish population (NEFSC[1]). These estimates of YOY bluefish abundance in 1994 and 1995 were used to calculate the daily consumption of bay anchovy by the YOY bluefish population in the following steps. First, the biomass of the spring- and summer-spawned cohorts on the shelf was calculated. This was done by determining the numbers in each spawning cohort (this was necessary because the VPA was for all YOY combined) based on relative abundance estimated from the NMFS autumn bottom trawl survey and then multiplying by the average individual fish weight in each cohort. Secondly, this cohort biomass was multiplied by the estimates of daily ration (lowest and highest) to determine the daily biomass of prey consumed by each cohort. To determine the amount of bay anchovy consumed daily, each cohort's biomass was multiplied by the mean proportion of bay anchovy by weight in each cohort's diet. Finally, a daily estimate of the numbers of bay anchovy consumed by the YOY bluefish population was calculated by dividing the biomass of bay anchovy consumed by the average bay anchovy weight ingested by each cohort. Bay anchovy weight was calculated from mean bay anchovy length ingested with regressions from Hartman and Brandt (1995a).

[1] NEFSC. 1997. Report of the 23rd Northeast Regional Stock Assessment Workshop (23rd SAW): Stock Assessment Review Committee (SARC) consensus summary of assessments. Northeast Fisheries Sci. Cent. Ref. Doc. 97-05, 191 p. [Available from National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026.]

Results

Dietary analyses

The stomach contents of 989 young-of-the-year (626 spring- and 363 summer-spawned) and 275 adult bluefish were examined. All YOY bluefish were captured between 12 and 29 September 1994 and 7 and 23 September 1995. Continental shelf bluefish diets were dominated by teleost fish and squid prey (see Table 1 for common and scientific names of bluefish prey).

In both 1994 and 1995, the dominant fish prey of spring-spawned bluefish in all three geographical regions was bay anchovy (Table 2). Other spring-spawned bluefish prey included long-finned squid, striped anchovy, butterfish, and round herring. Butterfish were slightly more important in 1994 than in 1995. Also in 1994, amphipods made up a substantial portion of spring-spawned bluefish diets in the SNE region. In 1995, channeled whelk were a relatively important prey of bluefish in the C–D region; the foot and operculum were found in bluefish collected over a large geographical area.

The dominant fish prey of summer-spawned bluefish across all geographical regions was bay anchovy in both 1994 and 1995 (Table 3). The incidence of long-finned squid in summer-spawned bluefish diets was low; however, other invertebrates such as

amphipods, mysids, crab larvae, and copepods were relatively important prey. This was particularly true for the relatively small size summer-spawned bluefish collected in the SNE in 1995; the diet of these fish were dominated by copepods (Table 3).

The diet of adult bluefish collected in the Georges Bank region was dominated by butterfish, squid, round herring, and Atlantic herring in both 1994 and 1995 (Table 4). There were several commercially important species consumed by adult bluefish on Georges Bank in 1994. These included American plaice, haddock, Atlantic cod, and several hake species. A large component of the diet of adult bluefish from Cape Hatteras to Montauk Point, NY, was bay anchovy. Butterfish, round herring, and squid were also important prey of bluefish collected from this geographical region. The diet of bluefish from both regions also included several other fish and invertebrate species (Table 4). Channeled whelk were preyed upon by adult bluefish in the same region and year that spring-spawned YOY bluefish were found to feed on them.

Table 1

Common and scientific names of bluefish prey items on the continental shelf and Georges Bank.

Common name	Scientific name
Fish	
American plaice	*Hippoglossoides plattessoides*
Atlantic cod	*Gadus morhua*
Atlantic herring	*Clupea harengus*
Atlantic mackerel	*Scomber scombrus*
Atlantic silverside	*Menidia menidia*
bay anchovy	*Anchoa mitchilli*
butterfish	*Peprilus triacanthus*
conger eel	*Conger oceanicus*
fawn cusk eel	*Lepophidium cervinum*
fourbeard rockling	*Enchelyopus cimbrius*
haddock	*Melanogrammus aeglefinus*
Northern pipefish	*Syngnathus fuscus*
Northern puffer	*Sphoeroides maculatus*
ocean pout	*Macrozoarces americanus*
planehead filefish	*Monacanthus hispidus*
red hake	*Urophycis chuss*
round herring	*Etrumeus teres*
sand lance	*Ammodytes* spp.
scup	*Stenotomus chrysops*
sea horse	*Hippocampus erectus*
searobin	*Prionotus* spp.
silver hake	*Merluccius bilinearis*
margined snake eel	*Ophicthus cruentifer*
spot	*Leiostomus xanthurus*
striped anchovy	*Anchoa hepsetus*
weakfish	*Cynoscion regalis*
white hake	*Urophycis tenuis*
windowpane	*Scophthalmus aquosus*
Invertebrates	
amphipods	*Gammarus* spp.
boreal squid	*Illex illecebrosus*
blue crab	*Callinectes sapidus*
cancer crab	*Cancer* spp.
channeled whelk	*Busycon canaliculatum*
fiddler crab	*Uca* spp.
lady crab	*Ovalipes ocellatus*
long-finned squid	*Loligo pealei*
mole crab	*Emerita talpoida*
sand shrimp	*Crangon* spp.

Net feeding

Although there was evidence of net feeding, it did not seem to bias diet indices. The percent occurrence of several different prey found to be "fresh" and the percent occurrence of these same prey found to be "digested" was similar (Table 5). Only in spring-spawned bluefish in the SNE region in 1995 were there more fresh prey than digested prey in their diet (30 fresh vs. 19 digested; Table 5). Spring-spawned bluefish had more freshly eaten prey in their diet (20–61%) than summer-spawned bluefish (0–26%).

Prey-type selectivity

Spring-spawned YOY bluefish selected positively ($\alpha > 1/m$) for bay anchovy in both 1994 (α=0.69, t-test vs. 0.25, t=8.05, df=154, P<0.001)) and 1995 (α=0.80, t-test vs. 0.33, t=6.40, df=74, P<0.001). However, YOY bluefish avoided ($\alpha < 1/m$) butterfish, squid, and "other" (determined for 1994 only) prey fish in 1994 (t-tests vs. 0.25; P<0.001) and 1995 (t-tests vs. 0.33, P<0.05) (Table 6).

Prey-size relationships and selectivities

There was a very weak but significant positive linear relationship between fish prey TL and YOY bluefish FL in 1994 (r^2=0.10, P<0.0001, n=418) and 1995 (r^2=0.02, P=0.027, n=224) (Fig. 1). A positive linear relationship also existed for fish prey TL and adult bluefish FL in 1994 (r^2=0.15, P<0.001, n=90) and 1995 (r^2=0.28, P<0.0001, n=100) (Fig. 2). Although there was a significant increase in mean prey sizes taken, juvenile and adult bluefish continued to take small prey with increasing body size.

Bay anchovy to bluefish FL ratios were higher in the summer-spawned bluefish cohort than in the spring-spawned cohort in 1994 and 1995. Additionally,

Table 2

Stomach contents of spring-spawned bluefish captured during the 1994 and 1995 National Marine Fisheries Service autumn bottom trawl survey. %*F*=proportion of bluefish stomachs containing a prey (±SE), %W=proportional contribution of identifiable prey to bluefish diet by weight (±SE). Note that proportions from cluster estimators do not add up to 100%. SE=standard error from variance estimators for cluster samples.

	1994						1995					
	Southern New England		Chesapeake–Delaware		South of Chesapeake		Southern New England		Chesapeake–Delaware		South of Chesapeake	
Prey type	%*F*	%W	%*F*	%W	%*F*	%W	%*F*	%W	%*F*	%W	%*F*	%W
Fish												
bay anchovy	71.4 (32.9)	45.7 (21.9)	35.7 (22.9)	40.4 (23.6)	25.0 (54.1)	6.0 (28.0)	57.2 (62.9)	83.2 (59.2)	50.2 (9.0)	50.1 (14.4)	47.4 (38.1)	43.8 (39.3)
butterfish	5.5 (3.4)	8.9 (6.0)	14.7 (7.5)	38.9 (19.0)	12.5 (97.5)	48.1 (375.2)	1.7 (8.8)	1.6 (9.4)			1.9 (4.5)	3.5 (8.2)
round herring	4.4 (2.4)	10.3 (7.6)					4.3 (3.1)	0.8 (5.7)	0.6 (0.9)	3.3 (5.5)		
striped anchovy	1.4 (3.1)	1.8 (4.2)	3.9 (4.9)	10.0 (10.8)	12.5 (123.9)	33.4 (331.1)	3.0 (16.8)	5.8 (29.3)	5.1 (3.3)	8.5 (5.7)	3.8 (6.3)	2.6 (4.6)
bluefish									1.1 (1.4)	2.9 (4.1)	1.9 (4.4)	4.2 (9.8)
silver hake	2.3 (6.0)	2.9 (7.6)										
seahorse									0.6 (0.9)	0.2 (0.3)		
margined snake eel											1.9 (4.4)	7.1 (16.2)
Serranidae											3.8 (5.9)	4.6 (8.9)
Sparidae											1.9 (4.2)	6.2 (13.6)
Clupeidae							0.4 (3.1)	1.8 (12.6)	0.6 (0.9)	2.8 (4.7)		
Unidentified fish	16.0 (10.8)		11.6 (5.6)		12.5 (97.5)		7.0 (27.2)		16.6 (5.6)		14.1 (9.3)	
Invertebrates												
long-finned squid	10.5 (7.4)	14.8 (16.0)	1.6 (2.0)	1.1 (1.7)			5.7 (25.6)	3.2 (13.0)	1.7 (1.6)	7.9 (9.6)	1.9 (9.3)	4.2 (7.2)
crab[1]	2.0 (3.9)	4.0 (10.6)									3.8 (6.6)	0.6 (1.0)
amphipods	31.2 (20.2)	11.1 (10.4)					3.0 (14.1)	1.9 (9.2)				
unidentified shrimp crustacean larvae[2]			1.6 (2.2)	0.9 (1.7)					2.2 (1.7)	0.6 (1.0)		
polychaete	1.4 (3.0)	<0.1 (0.3)	0.8 (1.4)	0.3 (0.5)								
channeled whelk									9.0 (8.1)	11.6 (9.3)		
Total stomachs analyzed	182		129		8		79		177		51	
Number containing prey	157		81		5		57		140		39	
Mean FL (mm, SE)	208 (2)		243 (4)		263 (14)		212 (2)		244 (3)		261 (3)	
FL range (mm)	161–270		161–300		200–300		180–300		160–300		200–300	
Mean wt (g, SE)	124.9 (3.5)		219.2 (9.4)		247.4 (33.8)		129.7 (5.0)		203.6 (7.3)		247.5 (9.3)	
Wt range (g)	51–256		49–398		116–343		75–342		50–371		105–365	

[1] Lady crab, mole crab, unidentified crab.
[2] Lady crab, *Penaeus* spp., unidentified crustacean larvae.

Table 3

Stomach contents of summer-spawned bluefish captured during the 1994 and 1995 National Marine Fisheries Service autumn bottom trawl survey. %*F*=proportion of bluefish stomachs containing a prey (±SE), %*W*=proportional contribution of identifiable prey to bluefish diet by weight (±SE). Note that proportions from cluster estimators do not add up to 100%. SE=standard error from variance estimators for cluster samples.

	1994						1995					
	Southern New England		Chesapeake–Delaware		South of Chesapeake		Southern New England		Chesapeake–Delaware		South of Chesapeake	
Prey type	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*
Fish												
bay anchovy	80.1 (30.1)	90.9 (7.1)	33.7 (72.5)	71.7 (70.0)	16.7 (250.0)	50.0 (750.0)	23.6 (113.5)	34.3 (145.7)	45.1 (32.3)	86.6 (33.5)	23.5 (72.6)	76.5 (253.4)
Atlantic silverside	0.3 (1.2)	0.9 (3.7)										
searobin larvae			8.1 (60.8)	0.8 (3.1)								
Unidentified fish	15.3 (9.9)		14.8 (23.1)		33.3 (0.0)		27.9 (33.1)		50.4 (32.5)		41.2 (63.6)	
Invertebrates												
long-finned squid	0.6 (2.1)	<0.1	3.6 (33.7)	1.4 (6.6)			1.7 (10.4)	1.7 (10.4)				
crab[1]	0.5 (2.0)	1.0 (3.7)										
crab larvae[2]	1.1 (4.0)	<0.1	12.4 (24.3)	3.7 (7.4)								
amphipods	19.1 (11.0)	7.0 (5.3)	3.9 (8.5)	0.8 (1.8)								
mysids			23.6 (139.6)	20.4 (71.2)	16.7 (250.0)	12.2 (182.4)						
copepods					16.7 (250.0)	8.7 (131.8)	44.7(149.1)	48.5 (186.0)				
sand shrimp	0.1 (0.5)	<0.1										
polychaete	<0.1	<0.1			16.7 (250.0)	29.1 (435.8)						
isopod			1.4 (10.1)	1.0 (3.6)								
Total stomachs	200		66		6		61		53		17	
Number containing prey	165		56		4		52		38		11	
Mean FL (mm, SE)	135 (1)		133 (2)		96 (12)		70 (3)		90 (3)		77 (3)	
FL range (mm)	86–160		107–160		37–120		20–140		60–150		60–100	
Mean wt (g, SE)	31.2 (0.9)		29.2 (1.4)		11.3 (2.4)		4.8 (0.6)		10.9 (1.3)		5.0 (0.6)	
Wt range (g)	6–64		10–53		1–19		0.1–32		2–45		3–12	

[1] Mole crab and unidentified crab.
[2] Lady crab, blue crab and fiddler crab.

Table 4

Stomach contents of adult bluefish captured during the 1994 and 1995 National Marine Fisheries Service autumn bottom trawl survey. %*F*=proportion of bluefish stomachs containing a prey (±SE), %*W*=proportional contribution of identifiable prey to bluefish diet by weight (±SE). Note that proportions from cluster estimators do not add up to 100%. SE=standard error from variance estimators for cluster samples.

	1994				1995			
	Georges Bank		Hatteras–Montauk		Georges Bank		Hatteras–Montauk	
Prey type	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*
Fish								
bay anchovy			25.9 (51.8)	21.4 (47.7)			36.4 (34.6)	34.9 (44.9)
butterfish	27.8 (28.7)	18.6 (23.6)	9.4 (18.5)	12.7 (30.0)	7.6 (38.0)	16.3 (80.2)	5.6 (12.0)	9.0 (20.8)
round herring	3.7 (9.2)	2.2 (5.6)	6.8 (17.4)	26.5 (87.9)	7.6 (41.8)	10.8 (66.4)	3.7 (9.1)	3.6 (11.1)
striped anchovy			1.8 (7.9)	1.7 (7.7)	2.2 (21.4)	5.2 (51.5)	3.9 (12.3)	5.0 (13.2)
bluefish							0.5 (2.3)	0.9 (4.7)
planehead filefish							0.5 (2.3)	0.2 (1.4)
Northern puffer							0.9 (4.6)	0.8 (4.0)
Northern pipefish	1.9 (7.5)	0.6 (2.5)						
searobin			1.8 (6.2)	2.1 (8.8)	2.2 (21.9)	6.5 (65.3)	0.5 (2.3)	1.1 (5.4)
weakfish			2.2 (7.8)	3.0 (12.9)			0.5 (2.3)	0.1 (0.6)
spot								
sand lance							0.5 (2.3)	0.9 (4.7)
scup			2.7 (7.9)	1.5 (4.5)			0.5 (2.3)	0.1 (0.5)
Atlantic herring	7.4 (17.6)	11.3 (23.7)			10.9 (54.7)	17.6 (85.0)	0.5 (2.3)	0.1 (0.7)
Atlantic mackerel			0.9 (4.2)	0.9 (4.3)				
fawn cusk eel							0.5 (2.3)	<0.1
conger eel							0.5 (2.3)	1.5 (7.2)
ocean pout			0.9 (4.3)	0.9 (4.3)	2.2 (22.9)	2.2 (22.9)	0.5 (2.3)	0.3 (1.7)
fourbead rockling	1.9 (7.5)	1.7 (7.0)						
American plaice	1.9 (7.6)	0.8 (3.5)						
windowpane	5.6 (22.0)	5.6 (22.0)			2.2 (21.9)	5.2 (51.9)		
silver hake	1.9 (7.6)	1.0 (4.2)			4.3 (39.5)	8.4 (76.3)		
white hake	1.9 (7.5)	2.4 (9.9)						
red hake	1.9 (6.7)	2.1 (7.6)					1.9 (7.4)	1.7 (6.7)
haddock	1.9 (7.5)	2.0 (8.0)			2.2 (21.9)	0.8 (8.4)		
Atlantic cod	3.7 (10.3)	6.7 (20.6)						
Gadidae	1.9 (7.6)	1.9 (7.6)						
Unidentified fish	29.6 (32.1)		26.1 (43.1)		30.4 (70.7)		21.9 (23.4)	
Invertebrates								
long-finned squid	29.6 (25.6)	23.7 (29.4)	11.6 (22.1)	5.2 (11.3)	15.2 (53.6)	18.1 (89.2)	7.7 (11.8)	10.9 (27.0)
boreal squid	11.1 (23.7)	8.4 (19.4)						
lady crab	3.7 (15.0)	1.2 (4.7)						
cancer crab	1.9 (7.2)	0.6 (2.5)						
unidentified crab			0.9 (4.1)	0.8 (3.5)	2.7 (22.9)	0.4 (3.7)	1.3 (4.6)	0.1 (0.4)
amphipods			0.9 (4.3)	0.9 (4.3)				
unidentified shrimp					4.3 (30.8)	2.0 (19.1)		
polychaete							2.0 (6.8)	4.9 (16.7)
channeled whelk							9.0 (33.2)	13.0 (41.9)
Total stomachs analyzed	50		65		44		116	
Number containing prey	45		45		32		84	
Mean FL (mm, SE)	653 (10)		451 (18)		607 (17)		391 (11)	
FL range (mm)	420–780		310–780		380–750		310–730	
Mean wt (g, SE)	3837 (151)		1546 (170)		3082 (225)		991 (106)	
Wt range (g)	1209–6151		368–5965		692–6530		319–4570	

the prey to predator FL ratios for summer-spawned bluefish were higher in 1995 than they were in 1994 (Fig. 3). Summer-spawned bluefish consumed relatively larger bay anchovies in 1995 than in 1994; this was due to both the smaller size of the summer-spawned cohort in 1995 and the larger bay anchovy prey. A linear function describing bluefish capture success as a function of prey length to bluefish length ratio from Scharf et al. (1998b) is also plotted in Figure 3 (capture success data for bluefish feeding on Atlantic silversides). The distribution of ratios for both spring- and summer-spawned bluefish in 1994 and spring-spawned bluefish in 1995 are values for which bluefish have relatively high capture success;

Table 5

The total number of prey (*n*) found either fresh or digested (fresh=no sign of digestion; digested=prey skinless to being only identifiable by skeleton or shape) in spring- and summer-spawned young-of-the-year bluefish stomachs and the percentage contribution of bay anchovy, striped anchovy, butterfish, and squid for these categories. Bluefish were captured during 1994 and 1995 National Marine Fisheries Service autumn bottom trawl surveys. Bluefish were collected from three geographical locations of the Mid-Atlantic Bight continental shelf (SNE=Southern New England, C–D=Chesapeake Bay to Delaware Bay, and SOC=South of Chesapeake Bay, after Munch 1997).

		Spring-spawned		Summer-spawned	
Location	Prey type	No. fresh (%)	No. digested (%)	No. fresh (%)	No. digested (%)
1994					
SNE	*n*	19	51	0	31
	bay anchovy	89.5	56.9		
	striped anchovy	5.3	7.8		
	butterfish	5.3	33.3		
	squid	0	2.0		
C–D	*n*	46	107	36	104
	bay anchovy	89.1	76.6	100	97.1
	striped anchovy	2.2	2.8	0	0
	butterfish	2.2	7.5	0	1.0
	squid	6.5	13.1	0	2.0
1995					
SNE	*n*	30	19	0	57
	bay anchovy	73.3	68.4		
	striped anchovy	6.7	10.5		
	butterfish	3.3	15.8		
	squid	16.7	5.3		
C–D	*n*	21	82	0	36
	bay anchovy	81.0	82.8		
	striped anchovy	19.0	13.8		
	butterfish	0	0		
	squid	0	3.4		

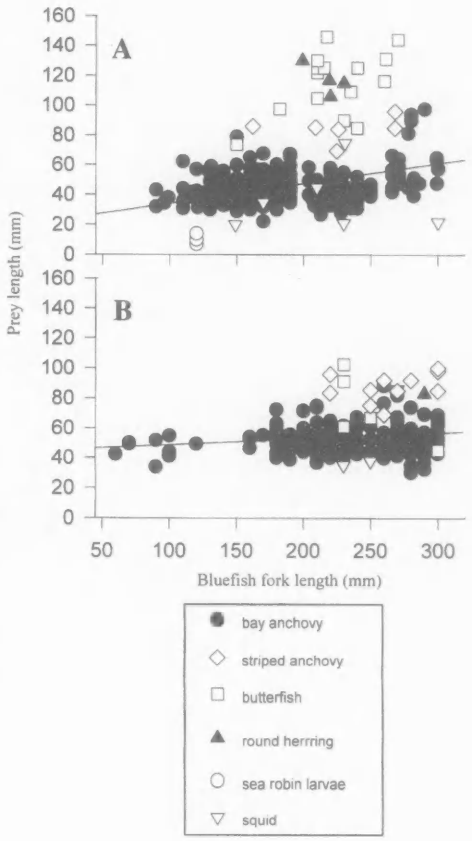

Figure 1

Prey total length (mantle length for squid) versus YOY bluefish fork length in (**A**) 1994 (*prey TL*=0.134 × *bluefish FL*+20.826, r^2=0.10, P<0.0001) and (**B**) 1995 (*prey* TL=0.041 × *bluefish FL*+44.538, r^2=0.02, P=0.027).

Table 6

Prey selectivity (Chesson's α, see text for calculations) in YOY bluefish collected on the U.S. east coast continental shelf in the autumn of 1994 and 1995. Values of α =1/m (where "m" is the number of prey categories) represent random feeding, whereas values of α > 1/m or α < 1/m represent "selection" and "avoidance" of prey, respectively. Values significantly different from 1/m (*t*-test, P<0.05) are indicated by a (+) for "selection" or (–) for "avoidance".

Prey type	1994 (1/m=0.25)	1995 (1/m=0.33)
Bay anchovy	0.69 (+)	0.80 (+)
Butterfish	0.12 (–)	0.03 (–)
Squid	0.09 (–)	0.18 (–)
Other	0.11 (–)	—

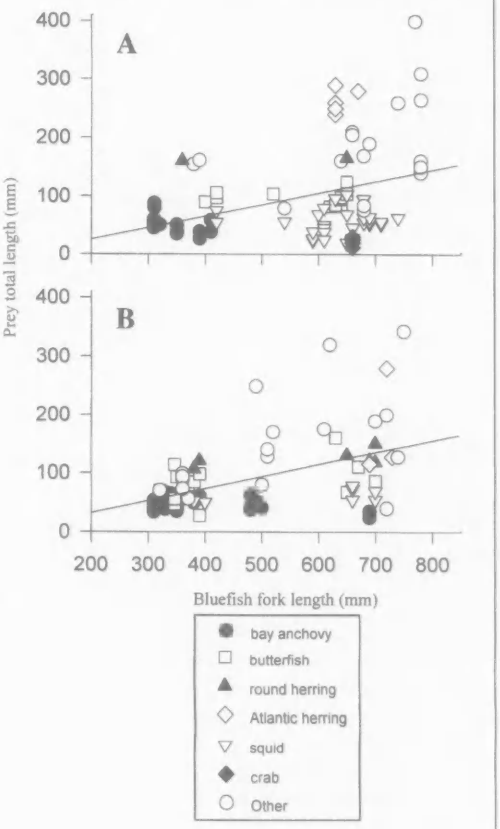

Figure 2

Prey total length (mantle length for squid) versus adult bluefish fork length in (**A**) 1994 (*prey TL*=0.199 · *bluefish FL*–14.413, r^2=0.15, P<0.001) and (**B**) 1995 (*prey TL*=0.205 × *bluefish FL*–9.047, r^2=0.28, P<0.0001). "Other" prey include searobin, red hake, silver hake, unidentified gadid, scup, windowpane, haddock, Northern puffer, conger eel, cusk eel, sand lance, striped anchovy, spot, weakfish, Atlantic mackerel, fourbeard rockling, and ocean pout.

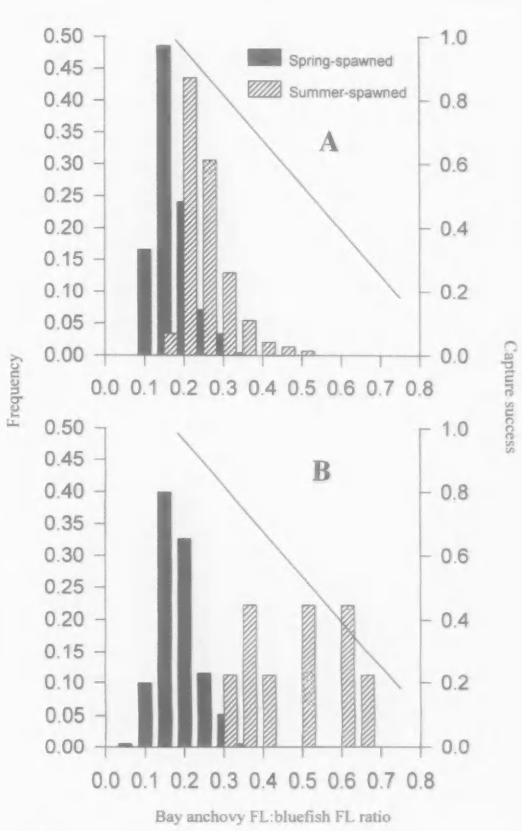

Figure 3

Bay anchovy FL to bluefish FL ratios for both spring-and summer-spawned bluefish in (**A**) 1994 and (**B**) 1995. Regression line for capture success versus prey length to predator length ratio from Scharf et al. (1998b).

however, the prey length to predator length ratios of summer-spawned bluefish in 1995 are values at which bluefish have relatively lower capture success (Fig. 3).

In 1994, there were four stations that had n>15 bay anchovy measurements for both spring and summer-spawned bluefish (n=16–20 bay anchovy measurements for summer- and n=22–39 for spring-spawned). Both spring- and summer-spawned YOY bluefish showed significant selection for relatively small bay anchovies (spring-spawned α=0.57 vs. 0.25, t=2.99, df=38, P=0.005; summer-spawned α=0.65 vs. 0.33, t=2.61, df=27, P=0.011) and avoidance of relatively larger anchovies in 1994 (spring-spawned α=0.02 vs. 0.25, t=3.83, df=38, P<0.001; summer-spawned α=0.07 vs. 0.33, t=2.86, df=27, P=0.006) (Table 7). Intermediate-size bay anchovy were taken in proportion to their abundance in 1994 (t-test; P>0.05 for all α's). In the 1995 analysis, three stations had n>15 individual bay anchovy lengths (n=17–32); an analysis of size-selective feeding of summer-spawned fish in 1995 was not possible owing to small sample size. Spring-spawned bluefish in 1995 showed no significant size selectivity (t-test; P>0.05 for all α's); however, the trend of increasing selectivity with decreasing prey sizes was present (Table 7).

Feeding chronology, daily ration estimates, and impacts on bay anchovy

Both spring- and summer-spawned YOY bluefish gut fullness values varied over the diel cycle in the different geographical regions of the MAB shelf. Peaks in gut fullness generally occurred at dawn, dusk, and diurnal time periods, whereas gut fullness values during nighttime collections were low in relation to diurnal gut fullness values (Fig. 4).

Table 7

Size-selectivity (Chesson's α, see text for calculations) for bay anchovy in YOY bluefish collected on the U.S. east coast continental shelf in the autumn of 1994 and 1995. Values of $\alpha = 1/m$ (where "m" is the number of prey categories) represent random feeding while values of $\alpha > 1/m$ or $\alpha < 1/m$ represent "selection" and "avoidance" of prey, respectively. Values significantly different from $1/m$ (t-test, $P<0.05$) are indicated by a (+) for "selection" or (–) for "avoidance".

	1994		1995	
Bay anchovy size (mm)	Spring-spawned ($1/m$=0.25)	Summer-spawned ($1/m$=0.33)	Spring-spawned ($1/m$=0.33)	Summer-spawned
25–34	0.57 (+)	0.65 (+)	—	—
35–44	0.27	0.28	0.44	—
45–54	0.14	0.07 (–)	0.37	—
55–64	0.02 (–)	—	0.19	—

Table 8

Daily ration g/(g · d) · 100 ±SE) and weighted mean temperature at which spring- and summer-spawned YOY bluefish were collected during National Marine Fisheries Service autumn bottom trawl survey in 1994 and 1995. Bluefish juveniles were collected from three geographical areas of the Middle Atlantic Bight continental shelf (SNE=Southern New England, C–D=Chesapeake Bay to Delaware Bay, and SOC= South of Chesapeake Bay, after Munch 1997). Daily ration was calculated using the Eggers' (1979) approach (see text). NA=not applicable due to low number of samples for diel series.

	Summer-spawned			Spring-spawned		
Year and geographical region	n	Temp. °C	Daily ration g/(g · d) · 100 (SE)	n	Temp. °C	Daily ration g/(g · d) · 100 (SE)
1994						
SNE	200	18.9	8.5 (3.1)	182	18.8	6.6 (2.5)
C–D			NA	129	20.0	4.8 (1.9)
1995						
SNE	61	20.7	12.4 (3.9)	79	19.9	3.7 (1.4)
C–D			NA	177	23.7	9.0 (2.9)
SOC			NA	51	24.3	8.1 (2.8)

In order to use the gut fullness data to estimate bluefish daily ration, gastric evacuation rate (GER) estimates were needed for bluefish at shelf water temperatures. The exponential GER model adequately described the evacuation of bay anchovy at 15°C from our laboratory experiment (r^2=0.87, n=22, $P<0.001$; Fig. 5). Incorporation of the 15°C GER estimate (R_e=0.102) into the evacuation rate vs. temperature function of Buckel and Conover (1996) gave the following equation: $R_e = 0.017\ e^{0.099\ Temp}$, n=16, r^2=0.82 (Fig. 5). The largest deviation from the equation describing R_e and temperature is from the single estimate of GER at 15°C. This is likely not due to differences in experimental protocol; the 15°C GER experiment was conducted identically to the experiments described in Buckel and Conover (1996). The larger deviation may result from there being only one estimate of GER at 15°C whereas each GER estimate for the higher temperatures represents a mean of four estimates (Fig. 5). Estimates of GER from this equation were used to estimate bluefish daily ration.

The daily ration of summer-spawned bluefish in the SNE region in 1994 and 1995 was 8.5 and 12.4 g/(g · d) · 100, respectively (Table 8). Spring-spawned bluefish daily ration estimates ranged from 4.8 to 6.6 g/(g · d) · 100 for the SNE and C–D region in 1994 and 3.7–9.0 g/(g · d) · 100 in the SNE, C–D, and SOC regions of the MAB in 1995. There was insufficient diel records to calculate feeding rates for the SOC region in 1994 or the remaining region and cohort combinations (Table 8).

The VPA estimates of YOY bluefish abundance in 1994 and 1995 were 24 million and 14 million, respectively. These estimations were partitioned into spring- and summer-spawned bluefish on the basis of relative abundances of these cohorts for each year (Table 9). It was estimated that spring-spawned bluefish consumed from 70 to 96 million bay anchovy per day in 1994 and from 68 to 170 million bay anchovy per day in 1995 during the September period of their migration (Table 9; the range is based on the lowest to highest daily ration estimate). Summer-spawned bluefish consumed 130 million bay anchovy per day in 1994 and 5 million per day in 1995 (there is no range for summer-spawned bluefish because there

was only one estimate of summer-spawned daily ration for each year).

Discussion

Dietary analyses

Bay anchovy was the predominant fish prey of both spring- and summer-spawned YOY bluefish in both 1994 and 1995. A previous gut contents analysis of NEFSC-NMFS bottom-trawl-collected bluefish (south of Cape Hatteras to Georges Bank) was conducted by Morris[2] from 1978 to 1980. Bay and striped anchovy dominated the diet of the 292 YOY bluefish (110–300 mm) that he examined; butterfish and squid were also important prey. The migration of YOY bluefish onto the shelf is thought to be controlled by declines in estuarine temperature and day length (Olla and Studholme, 1972). Schools of bay anchovy migrate out onto the shelf beginning in September and are concentrated off New York, New Jersey, and the Delmarva peninsula in the autumn (Vouglitois et al., 1987) in a similar pattern to that of concentrations of YOY bluefish (Munch and Conover, in press). The timing of bluefish estuarine emigration may be linked with bay anchovy movements offshore.

Invertebrates were an important part of the diet of YOY bluefish in several regions. In 1994, there was a large amount of gammarid amphipods in the diets of spring- and summer-spawned bluefish in the SNE region. In addition, mysids contributed to the diet of summer-spawned fish in the C–D and SOC regions of the continental shelf in 1994. Diets of juvenile bluefish in estuaries are usually dominated by fish prey, but at times invertebrates, such as shrimp, are a major prey (Friedland et al., 1988; Juanes and Conover, 1995). This pattern is likely a function of prey availability and prey size. Bluefish prey selectivity was related to prey abundance in the Hudson River (Buckel et al., 1999). Bay anchovy schools and invertebrate swarms are likely to have patchy distributions on the shelf; the diet of bluefish at any location will be dependent on local prey availability.

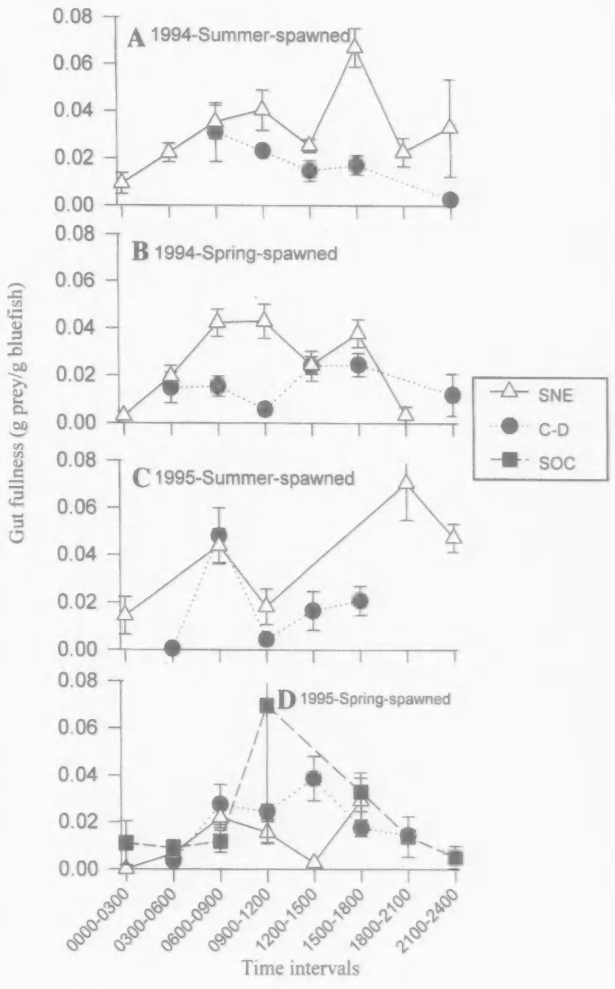

Figure 4

Gut fullness (g prey/g bluefish) for spring-and summer-spawned bluefish collected from SNE, C–D, and SOC regions of the continental shelf in 1994 (**A, B**) and 1995 (**C, D**) versus time interval of collection. Sunrise fell between the 0600 and 0900 time interval and sunset fell between the 1800 and 2100 time interval. Error bars are ±1 SE.

Channeled whelk has not been reported previously as a prey of bluefish. The foot of channeled whelk with the operculum still attached was found in several bluefish in the C–D region in 1995. This may have been due to opportunistic feeding on whelk that had shell damage related to some fishery activity. However, whelk occurred in bluefish gut contents over a fairly broad geographic area and not at a single

[2] Morris, T. L. 1984. Food of bluefish. Woods Hole Laboratory Reference Document 84-22, Woods Hole Laboratory, Northeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA 02543 MED/NEFC 84-26, 13 p.

station (Cape May, NJ, to Lewes, DE). Bluefish may attack whelk when the foot is extended out of the shell and may sever that section alone. This would explain the presence of only the foot portion of the animal.

Summer-spawned bluefish diet was dominated by copepods in the SNE region in 1995. Marks and Conover (1993) found that the diet of summer-spawned bluefish collected in surface waters of the New York Bight was dominated by copepods. Summer-spawned bluefish size ranged from 17 to 64 mm TL in their samples and ranged from 20 to 140 mm FL in our samples from the SNE region in 1995. The large presence of copepods in this cohort's diet compared with other regions on the shelf in 1995 and with summer-spawned bluefish diets in 1994 is most likely a result of their small size (see "Prey-size analysis" section).

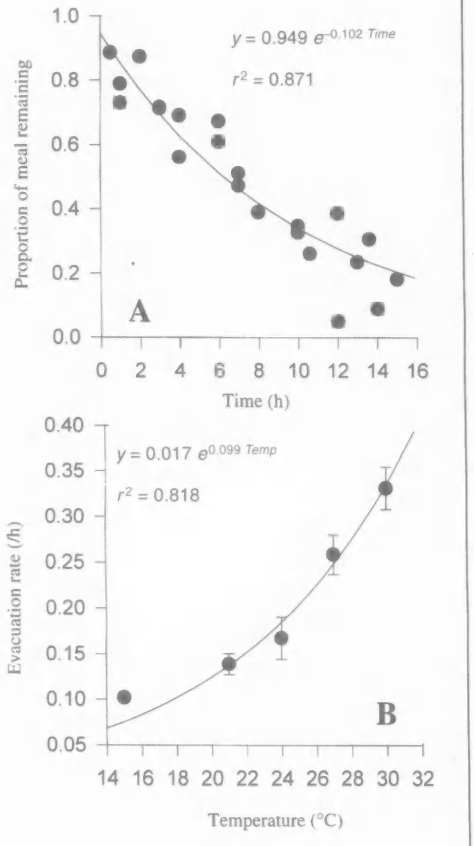

Figure 5

(**A**) Proportion of meal remaining vs. time for bluefish fed a single bay anchovy meal at 15°C (*proportion of meal remaining* = $0.949\ e^{-0.102 \cdot time}$), and (**B**) YOY bluefish evacuation rate versus temperature (data for temperatures of 21 to 30°C are from Buckel and Conover, 1996; *evacuation rate*=$0.017e^{0.099 \cdot temp}$). Error bars are ±1 SE.

McBride et al. (1995) found that age-0, spring-spawned bluefish abundance appeared to be regulated by density-dependent (compensatory) losses in Narragansett Bay, Rhode Island. One potential density-dependent mechanism is cannibalism. There were very few cases of bluefish cannibalism on the continental shelf; spring-spawned bluefish cannibalism of summer-spawned bluefish occurred in the C–D and SOC region in 1995, a year when individuals in the summer-spawned cohort were relatively small in size. However, past diet studies of bluefish have found a higher incidence of cannibalism, particularly off the Carolinas (Lassiter, 1962; Naughton and Saloman, 1984). Bluefish abundance is currently low (NEFSC[1]) and cannibalism may be frequent only when bluefish are more abundant or other prey abundances are low.

We found slight regional differences in the diet of adult bluefish; diets of bluefish in 1994 and 1995 were similar to those found in past studies. In the Georges Bank region in 1994 and 1995, the dominant prey of adult bluefish were butterfish, long-finned squid, boreal squid, round herring, and Atlantic herring. Bay anchovy, butterfish, round herring, and long-finned squid were the dominant prey of adult bluefish collected from Cape Hatteras, NC, to Montauk Point, NY. Morris (1984) found that long-finned squid, boreal squid, butterfish, round herring, and bay and striped anchovies dominated the diet of adult bluefish (n=226) captured in NEFSC-NMFS bottom trawls (1978–80, spring, summer, autumn combined) from these same regions. Richards (1976) examined the diet of adult bluefish angled near Long Island, NY, in the summer and autumn. The diet of bluefish in this area included bay anchovy, long-finned squid, menhaden (*Brevoortia tyrannus*), butterfish, and silver hake (n=66, FL range: 490–750 mm).

There were very few bluefish for our diet analysis from south of Cape Hatteras; however, Naughton and Saloman (1984) collected 729 bluefish from this region using hook and line during 1977–81 and reported the diet of bluefish in this area as dominated by Scianidae, Clupeidae, Mugilidae, Labridae, and Atherinidae. Scianids, clupeids, engraulids, sparids, atherinids, and squids were important prey in Lassiter's (1962) study of over 900 bluefish captured by beach haul seining or hook and line August–December 1960 and March, June–August 1961. The diet of bluefish (n=42) collected south of Cape Hatteras in the autumn by bottom trawling was dominated by squid, butterfish, and striped anchovy (Morris, 1984).

There were several commercially important groundfish species in the diet of adult bluefish on Georges

Table 9

Estimated spring- and summer-spawned bluefish daily consumption of bay anchovy on the U.S. east coast continental shelf in the autumn of 1994 and 1995. We used mean size of bluefish, daily ration estimates, proportion of bay anchovy in the diet, and mean bay anchovy size that were measured for each cohort in this study. Estimates of the numbers of YOY bluefish for 1994 and 1995 are from virtual population analysis (VPA) performed by NEFSC (see Footnote 1 in main text); we partitioned the numbers between spring- and summer- spawned bluefish using relative abundances of each cohort from the NEFSC-NMFS autumn groundfish survey cruises.

Cohort	Bluefish numbers	Biomass of bluefish cohort (10^6 kg)	Amount of bay anchovy consumed daily (kg/d; low ration)	Amount of bay anchovy consumed daily (kg/d; high ration)	Number of bay anchovy consumed daily (no./d; low)	Number of bay anchovy consumed daily (no./d; high)
1994						
Total	24×10^6					
Spring-spawned	7.2×10^6	1.20	25,000	34,000	70×10^6	96×10^6
Summer-spawned	16.8×10^6	0.50	35,000		130×10^6	
1995						
Total	14×10^6					
Spring-spawned	9.8×10^6	1.86	45,000	110,000	68×10^6	170×10^6
Summer-spawned	4.2×10^6	0.032	2,000		5×10^6	

Bank in 1994. Morris (1984) also found gadids in stomach contents of adult bluefish. This finding is of interest because there is a large effort to understand the factors that regulate fish populations on Georges Bank (Peterson and Powell, 1991). The biomass of skates (Rajidae) and dogfish sharks (Squalidae) has increased in this area of the shelf and in some locations makes up the largest part of fish biomass (Overholtz et al., 1991). However, cartilaginous fishes were not found in the diet of adult bluefish. Bluefish predation will have no direct effect in regulating the population sizes of these fishes. However, bluefish may play a role in the recovery of commercially important groundfish species on Georges Bank. Because bluefish distribution is closely linked with temperature (Munch, 1997), an increased warming trend may allow a larger proportion of the bluefish population to extend northward onto Georges Bank. Ware and McFarlane (1995) found that Pacific hake (*Merluccius productus*) biomass and hake predation on herring (*Clupea harengus*) increased with recent increases in temperature off the west coast of Vancouver Island. They concluded that this recent increased predation explains recent declines in the herring stock. The importance of bluefish predation to recovery of groundfish species warrants further investigation.

Net feeding

Postcapture net-feeding can bias diet indices and gut fullness level estimates. Net feeding is known to occur in a variety of Pacific midwater fish (Lancraft and Robison, 1980). There was little evidence that net feeding biased our estimates of bluefish diet given the similarities between percent of fresh versus digested prey; however, any net feeding would lead to biased estimates of gut fullness level and inflated estimates of consumption rate. Lancraft and Robison (1980) found that larger fish were more likely to ingest artificial prey. The larger spring-spawned cohort had more fresh prey in its diet than the smaller summer-spawned bluefish which may be a result of a higher incidence of net feeding by this cohort.

Prey-type selectivity

Spring-spawned YOY bluefish selected for bay anchovy over all other prey types in both 1994 and 1995. Butterfish, squid, and "other" potential prey were avoided. This is most likely due to both the relative abundances of these prey as well as interspecific size differences. Bay anchovy tended to be the smallest prey available; the only smaller prey of spring-spawned bluefish were invertebrates such as amphipods (ranging from 3 to 15 mm TL). In the Hudson River estuary, the prey with the highest relative abundance were selected for, whereas the prey with the lowest abundance were selected against (Buckel et al., 1999). A second possible explanation for the strong selection of bay anchovy could be sampling bias. Chesson's (1978) index assumes that prey abundance is large in relation to the amount consumed (likely true for the shelf) and that the

catchability or availability of the different prey groups to the trawl are the same. We do not have estimates of the catchability for each of the prey species used in this analysis. Our results would be biased if these differ. For example, catchabilities for squid and butterfish may be higher than that of bay anchovy and may explain the strong selection for bay anchovy.

Prey-size analysis

Although there was a weak positive linear relationship between ingested bluefish prey sizes and bluefish length, it was mainly due to prey other than bay anchovy. The slope of the regression of bay anchovy length on bluefish length alone was 50% and 75% less than the slope of the regression of all prey on bluefish length in 1994 and 1995, respectively. The sizes of bay anchovy taken by the smallest YOY bluefish were similar to those taken by the largest YOY bluefish, especially in 1995. Juanes and Conover (1995) and Scharf et al. (1997) saw a similar relation for bluefish feeding on piscine prey in New York estuaries.

Most ratios of bay anchovy length to bluefish length were similar to those seen in past estuarine work (Juanes and Conover, 1995; Scharf et al., 1997). Juanes and Conover (1995) hypothesized that the shift in spring-spawned bluefish diet from Atlantic silversides to bay anchovy in Great South Bay, NY, was a result of the higher capture success on the relatively smaller bay anchovy. The capture success of bluefish feeding on bay anchovy is likely higher than that of bluefish feeding on the relatively larger butterfish and squid. Our size selectivity analysis shows that even within bay anchovy there is preference for smaller sizes (Table 7).

The relatively small size of the 1995 SNE summer-spawned bluefish (1994 mean FL=135 vs. 1995 mean FL=70) influenced the extent of piscivorous feeding in this cohort. The capture success was plotted for bluefish feeding at different ratios of prey length to bluefish length from laboratory work on Atlantic silversides (Scharf et al., 1998b). Summer-spawned, small-size bluefish in 1995 would have experienced greatly reduced capture success when feeding on bay anchovy.

Feeding chronology, daily ration estimates, and impacts on bay anchovy

Bluefish appear to feed mainly during the day or at dawn or dusk. This was also noted in past work on juvenile bluefish in estuarine environments (Juanes and Conover, 1994; Buckel and Conover, 1997). In the Hudson River estuary, the diel feeding patterns of bluefish appeared to be linked to their diel movement patterns (Buckel and Conover, 1997). This may also be the case for shelf bluefish; Munch (1997) found that the catch per unit of effort (CPUE) of YOY bluefish in NEFSC-NMFS bottom trawl collections was significantly higher in diurnal than in nocturnal collections. Munch (1997) hypothesized that this diel movement to near bottom habitat (which makes them available to bottom trawling) during the day may be in response to the vertical migration of bay anchovy. Bay anchovy exhibit diel vertical migration and are significantly more available to bottom trawl sampling during the day compared with at night (Vouglitois et al., 1987).

Our daily ration estimates for spring-spawned bluefish (3.7–9.0 g /(g · d) · 100) are similar to past estimates of daily ration for September. Measurements of bluefish maximum daily ration from a laboratory mesocosm experiment (18.5–23°C) for mid-September were ~10 g/(g · d) · 100 (Buckel et al., 1995). Field estimates of bluefish daily ration in the Hudson River estuary were 10.1–12.6 in mid to late August and 7.3 in mid-September (Buckel and Conover, 1997). Mean spring-spawned bluefish size was larger and mean temperatures were slightly lower on the shelf compared with bluefish sizes and temperatures in the above laboratory and field experiments. This finding may explain our slightly lower daily ration estimates for spring-spawned bluefish on the shelf in the autumn. Hartman and Brandt's (1995b) laboratory estimates of maximum daily ration (C_{max}) are also similar to our field estimates of spring-spawned bluefish daily ration estimates on the shelf. From their experiments, estimates of C_{max} for bluefish ranging from 100 to 350 g at 20°C (temperature at which bluefish were found on the shelf) are 7.5 to 12.5 g/(g · d) · 100.

Owing to low sample sizes and an inadequate diel record, the daily ration of summer-spawned bluefish was determined only in the SNE region in 1994 and 1995. The daily ration estimate in 1994 was lower at 8.5 g/(g · d) · 100 than the estimate of 12.5 g/(g · d) · 100 in 1995. The mean size of fish in this cohort varied substantially between 1994 (31.2 g) and 1995 (4.8 g). The size and the temperature difference (1994= 18.9°C vs. 1995=20.7°C) may explain the differences in daily ration. The daily ration estimates of these fish are slightly lower than would be predicted from laboratory estimates of maximum daily ration of bluefish at these sizes and temperatures (Buckel et al., 1995; Hartman and Brandt, 1995b); however, both shelf estimates fall into the 95% confidence interval of the summer-spawned bluefish daily ration estimate (19–20 September 1992) in the Hudson River (Buckel and Conover, 1997).

For our estimates of bay anchovy consumption by the YOY bluefish population during their September migration, it was assumed that the entire YOY bluefish population occurred on the shelf from Cape Hatteras, NC, to Montauk, NY. Support for this comes from sharp declines in YOY bluefish CPUE in early autumn estuarine beach seine surveys (Nyman and Conover, 1988; McBride and Conover, 1991) and an abrupt decline in average bluefish size on the shelf during early autumn (Munch, 1997). Our estimates show that given a 30-d migration period in September, the population of YOY bluefish could consume from 6.0 to 6.8 billion bay anchovies in 1994 and from 2.2 to 5.3 billion in 1995.

Summer-spawned bluefish consumed two orders of magnitude less bay anchovy per day in 1995 (5 million) compared with 1994 (130 million). This was partly due to the low abundance of this cohort in 1995 (4.2 million) compared with that in 1994 (16.8 million). The amount of bay anchovy in the diet of summer-spawned bluefish (80% in 1994 vs. 60% in 1995) and the absolute size of bay anchovy prey taken by the two cohorts (0.27 g in 1994 vs. 0.54 g in 1995) explained the remainder. Interannual variation in the size structure of the summer-spawned cohort and their predominant piscine prey (bay anchovy) can have dramatic effects on the predatory impact of this bluefish cohort on bay anchovy populations. Although the importance of size-dependent processes in freshwater fish predator-prey interactions is well described (Kerfoot and Sih, 1987; Ebenman and Persson, 1988), their importance for piscivore-prey interactions in marine systems is just beginning to be recognized (Juanes and Conover, 1995).

There are no estimates of coastwide bay anchovy abundance for 1994 and 1995; hence, no direct examination of the impact of this estimated bay anchovy loss to the continental shelf bay anchovy population was made. There are bay anchovy biomass density estimates for estuaries on the east coast of the U.S. Vouglitois et al. (1987) estimated that the bay anchovy standing crop in Barnegat Bay, NJ, ranged from 830 to 4830 kg/km^2. In Chesapeake Bay, Luo and Brandt's (1993) bay anchovy biomass density estimate for September was ~8000 kg/km^2. We calculated the standing stock of bay anchovy on the shelf by multiplying the estimated ranges of estuarine bay anchovy densities by the area (km^2) in which bluefish were collected on the shelf. This area (km^2) estimate was calculated by summing all the NEFSC stratum areas in which YOY bluefish were captured in the autumn groundfish survey in 1994 and 1995.

During the month of September, bluefish (spring- and summer-spawned combined) consumption of bay anchovy could account from ~2 to 22% of bay anchovy standing stock in 1994 and from 1% to 24% of the bay anchovy standing stock in 1995. Bay anchovy are probably less dense on the shelf than in the estuary and our estimates of bluefish impact may be underestimates. However, the latest bluefish stock assessment (Mid-Atlantic Fishery Management Council[3]) has found that bluefish abundance may be lower than that reported in the VPA (NEFSC[1]). This could mean that our impact estimates are overestimates. At the upper range of the impact estimates, it is clear that the YOY bluefish population on the continental shelf consume a significant quantity of bay anchovy biomass. The effect of this loss on the population dynamics of bay anchovy or the fish community on the continental shelf is unknown.

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Abstract.—The bluefish, *Pomatomus saltatrix*, has long been considered a key predator on U.S. east coast fish species. Many of its prey species are also landed by humans, but no comparison of prey biomass harvested by bluefish versus fishermen has been attempted previously. We used data on growth, mortality, gross growth efficiency, and abundance to model the total prey consumption rate by bluefish at the population level. This estimate and previously published information on diet were used to calculate the biomass of individual resource species "harvested" by bluefish. The prey biomass consumed by bluefish annually along the U.S. Atlantic coast is equal to eight times the biomass of the bluefish population. Bluefish consume a much higher biomass of squid and butterfish than is currently harvested by commercial fisheries for these species. Bluefish consumption of Atlantic menhaden, however, was below the current fisheries landings for this species. For resource species that are shared with bluefish, our findings highlight the need for multi-species assessment and management.

Mutual prey of fish and humans: a comparison of biomass consumed by bluefish, *Pomatomus saltatrix*, with that harvested by fisheries*

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The bluefish, *Pomatomus saltatrix*, has long been regarded as one of the most voracious piscivores of the western North Atlantic. In 1873 the U.S. Commissioner of Fisheries, S. F. Baird, stated in a report to congress that: ". . . I am quite inclined to assign to the bluefish the very first position among the most injurious influences that have affected the supply of fishes . . . a daily loss of 25 hundred million pounds . . . their trail is marked by fragments of fish and the stain of blood . . ." (Baird, 1873). Baird was concerned with the possibility that the high abundance of bluefish during that period was the cause of concomitant declines in fish landings.

Bluefish abundance along the U.S. Atlantic coast has been known to fluctuate dramatically over the past two centuries (Bigelow and Schroeder, 1953). The impact of variations in bluefish abundance on their principal prey as well as on the community structure of the continental shelf as a whole may be substantial (Clepper, 1979; Kerfoot and Sih, 1987). If the major prey of bluefish are also harvested by humans, then the potential fishery landings of such species may be influenced strongly by bluefish abundance. Moreover, species management through adjustment of the fishing effort will likely be ineffective if the amount of prey consumed by a key natural predator is substantially larger than the landings and ignored as a variable component of natural mortality.

In this study, we estimate the total prey biomass consumed annually by a given biomass of bluefish using a model developed by Pauly

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(1986). Previously published data on diet and recent estimates of bluefish population size along the U.S. Atlantic coast were used to determine the "harvest" of prey by bluefish. We then compared "harvesting" of prey by bluefish to the biomass harvested by the fishery for the east coast as a whole. Prey consumption by age class was calculated to determine at which age the largest impact on prey occurs. We present these analyses not as management tools but merely as gross estimates of the probable magnitude of the bluefish harvest of fishery species so as to stimulate more detailed studies.

Methods

Estimates of population consumption rate

The total U.S. east coast bluefish population consumption of a given prey was calculated from estimates of diet, the biomass of the bluefish population, and food consumption rate. Bluefish diet information was available from the literature for various seasons and regions along the east coast (Lassiter, 1962; Richards, 1976; Buckel et al., 1999a; Morris[1]; Naughton and Saloman[2]). Bluefish biomass estimates were available for 1982 to 1995 from a virtual population analysis (VPA) performed by the Northeast Fisheries Science Center, National Marine Fisheries Service, Woods Hole, MA (NEFSC[3]). However, estimates of bluefish consumption rate were available only for young-of-the-year (YOY) (Juanes and Conover, 1994; Buckel et al., 1995; Buckel and Conover, 1997) or for age-0 to age-2 bluefish in Chesapeake Bay (Hartman and Brandt, 1995a). For this reason, we used the approach described below.

The quantity of food consumed annually by the bluefish population was estimated by using Pauly's (1986) age-structured consumption rate model. The model is based on a growth function (e.g. von Bertalanffy growth function, VBGF), the instantaneous total mortality rate (Z), and the relationship of gross growth efficiency to weight. Pauly's (1986) model in simplified form is

$$\frac{Q}{B} = \frac{\int_{t_r}^{t_{max}} \frac{(dw/dt) \times N_t}{K_{w(t)}}\, dt}{\int_{t_r}^{t_{max}} W_t \times N_t\, dt},$$

where Q/B is the food consumption per unit population biomass (see descriptions in Pauly (1986), Pauly and Palomares (1987), and Palomares and Pauly (1989)). The numerator of the model represents the food consumption of the population (Q), which is determined from the growth increment (dw/dt), numbers of fish at age t (N_t, determined from an initial arbitrary number of recruits), and the growth efficiency (K_1) for a given weight at age t. Values are integrated over age classes from t_r to t_{max} (age at recruitment to a maximum age). The denominator is the biomass term (B) which is the weight of individual fish at age t (W_t) multiplied by the number of fish (N_t) at age t. This value is integrated over all cohorts from t_r to t_{max}. An annual Q/B estimate represents the number of times the population consumes its own weight per year (Pauly, 1986).

Pauly and Palomares (1987) have provided a BASIC program to calculate Q/B from VBGF parameters, a parameter from the relationship describing K_1 as a function of weight, and an estimate of total mortality (Z). Growth for the Q/B model is based on the VBGF model expressed in weight form:

$$W_t = W_\infty \times \left[1 - e^{-k \times (t - t_0)}\right]^b,$$

where t = time in years;
W_t = weight of bluefish at age t;
W_∞ = asymptotic weight;
k = growth coefficient;
t_0 = age at weight zero; and
b = exponent of the length-weight relationship (i.e. $W = aL^b$).

For bluefish, Wilk's (1977) VBGF parameters were used where $k = 0.226$, $t_0 = -0.123$, $W_\infty = 8725$g, and $b = 3$ (Wilk's estimate of b was 2.89 but $b = 3$ was used owing to ease of use in Pauly's (1986) model).

The Q/B model assumes that gross growth efficiency (K_1) data depends on weight (W) according to

$$K_1 = 1 - (W/W_\infty)^\beta$$

To estimate β for use in the calculation of Q/B, bluefish gross growth efficiency and weight data from experiments on YOY fish described in Buckel et al. (1995) were used. The linearized form of the above model described in Pauly (1986) was fitted to the data

[1] Morris, T. L. 1984. Food of bluefish. Woods Hole Ref. Doc. 84-22, 13 p. [Available from Woods Hole Laboratory, Northeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA 02543.]

[2] Naughton, S. P., and C. H. Saloman. 1984. Food of bluefish (*Pomatomus saltatrix*) from the U.S. south Atlantic and Gulf of Mexico. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SEFC-150, 37 p.

[3] NEFSC (Northeast Fisheries Science Center). 1997. Report of the 23rd Northeast Regional Stock Assessment Workshop (23rd SAW) Stock Assessment Review Committee (SARC) consensus summary of assessments. Northeast Fisheries Sci. Cent. Ref. Doc. 97-05, 105 p.

to estimate β (β=–0.0445, r^2=0.64, F=45.44, df=1,25, P<0.0001).

The current stock assessment of bluefish assumes a natural mortality of M=0.25. The highest fishing mortality (F) measured on the east coast bluefish population was in 1992 at 0.51 and recent estimates of F are around 0.4–0.5 (NEFSC[3]). Therefore, an estimate of $M + F$=0.75 was used as a total mortality (Z) input into the Pauly (1986) model to estimate Q/B. The value of Z does not affect the estimate of Q/B dramatically because of its presence in both the numerator and denominator of the equation (see above). Annual consumption (Q/B) was estimated for bluefish from age-0 to age-10.

To determine if our estimate was robust, Hartman and Brandt's (1995a) equation ($C_{max} = 0.520 \times W^{-0.288}$) describing laboratory (20–25°C) estimates of maximum consumption rate (C_{max}, g/(g · d)) as a function of bluefish weight (W, g) was also used to calculate the population consumption for 1995. First, bluefish biomass by age class was calculated by multiplying bluefish numbers at age (NEFSC[3]) by the mean bluefish weight at age (W_t calculated from Wilk's (1977) VBGF function and length:weight conversion equation; $W_{age\,0}$ was estimated at t=0.5). Second, the maximum consumption rate was calculated for a mean bluefish weight at age from the relationship between C_{max} and bluefish weight provided by Hartman and Brandt (1995a). To do so, we extrapolated out beyond the range of fish sizes used in their laboratory experiment, assuming that values obtained in this way were accurate. Lastly, these age-specific consumption rates were then multiplied by the biomass of each age class. Summing across age classes provided us with a maximum biomass of prey consumed by the bluefish population at 20–25°C; this value was divided by the biomass of the population to obtain a daily Q/B value. To calculate an annual Q/B value, the daily Q/B value was multiplied by 365 days. Additionally, this Q/B value was temperature adjusted from 22.5°C to 17.5°C. This was done by multiplying by the ratio of bluefish consumption rate estimated at 17.5°C (average temperature for coastal bluefish [Munch, 1997]) to consumption rate estimated at 22.5°C (temperature of Hartman and Brandt's [1995a] study). This ratio was estimated from both Buckel et al. (1995) and Hartman and Brandt (1995a) data and in both cases was found to be ~0.60.

Impact by age class

From the above analysis, the age class where total biomass consumption peaks can be determined. This calculation was first made for a simulated bluefish population having constant recruitment (N=1 × 10[7]) and total mortality (Z=0.75, see above). However, bluefish exhibit highly variable recruitment across years. To illustrate the impact of variable age structure, we also calculated biomass consumed by age class on the basis of actual abundances in 1984 (a year when preceding recruitments had been fairly constant and age structure was typical) and in 1995 (a year when preceding recruitments were highly variable and age structure was unstable).

Comparison of biomass consumed by bluefish with that harvested by fisheries

The estimate of the annual amount of prey consumed by the western Atlantic bluefish population is the annual Q/B estimate (described above) multiplied by stock biomass. The prey consumption for three different population biomass sizes was estimated based on VPA estimates; these were the minimum, maximum, and average population sizes from 1982 to 1995 (NEFSC[3]). The total annual consumption at these three stock sizes was estimated for Atlantic butterfish (*Peprilus triacanthus*), long-finned squid (*Loligo pealei*), boreal squid (*Illex illecebrosus*), and Atlantic menhaden (*Brevoortia tyrannus*). These are primary species in the diet of bluefish that are also landed by fishermen.

Several studies were used to attribute the total biomass consumption by bluefish to different geographic regions, seasons, and prey species. To simulate the migratory patterns of bluefish, it was assumed that 100% of the population was north of Cape Hatteras during summer and autumn and 100% of the population was south of Cape Hatteras during spring and winter. Diet data from Richards (1976), Morris[1], and Buckel et al. (1999b) were used to describe bluefish diet in the summer and autumn north of Cape Hatteras. The diet studies of Naughton and Saloman[2] and Lassiter (1962) were used to describe bluefish diet south of Cape Hatteras (Carolinas and southeast Florida) during winter and spring. Details regarding these diet studies can be found in Buckel et al. (1999b).

To calibrate the relative importance of bluefish predation on squid, butterfish, and menhaden, the annual bluefish consumption of these prey was plotted along with the average, minimum, and maximum fisheries landings (1984–92) for these species as compiled by the National Marine Fisheries Service (Anonymous[4]).

[4] Anonymous. 1993. Fisheries of the United States, 1992. U.S. Dep. Commer., National Oceanic and Atmospheric Association, National Marine Fisheries Service, Silver Spring, MD, 115 p.

Table 1

Estimate of daily and annual prey consumption of the 1995 bluefish population by age class. We used weight-at-age data from Wilk,[1] maximum consumption rate estimates from Hartman and Brandt (1995a), and the virtual population analysis (VPA) estimates of bluefish number by age from NEFSC (see Footnote 3 in main text).

Age	Bluefish weight (kg)	Bluefish numbers (millions)	Bluefish biomass (10^6 kg)	Consumption rate (kg/(kg · d))	Biomass of prey consumed daily (kg)
0.5	0.031	13.89	0.43	0.1941	82538
1	0.143	17.47	2.50	0.1245	311317
2	0.662	4.78	3.16	0.0801	253240
3	1.502	3.95	5.92	0.0633	374750
4	2.524	2.86	7.22	0.0545	393250
5	3.604	3.31	11.92	0.0492	585820
6	4.654	5.88	27.35	0.0456	1249322
7	5.622	2.76	15.53	0.0432	671889
8	6.481	1.55	10.03	0.04152	416561
9+	7.225	3.99	28.84	0.0402	1160642
		Sum of bluefish biomass (B; 10^6 kg)	112.90	Sum of biomass consumed (Q; kg)	5499328
				Q/B daily (at 22.5°C)	0.0487
				Q/B annual (at 22.5°C)	17.78
				Q/B annual (at 17.5°C)	10.84

[1] Wilk, S. J. 1977. Biological and fisheries data on bluefish, *Pomatomus saltatrix* (Linnaeus). Tech. Ser. Rep. 11, 56 p. [Available from James J. Howard Marine Sciences Laboratory, Northeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 74 Magruder Rd., Highlands, NJ.]

Effects of pooling diet across ages

One potential shortcoming of this analysis was the use of diet data pooled across age or size groups. This procedure was unavoidable because of the lack of data describing bluefish diet by age or size for different seasons and geographical locations on the east coast of the United States. The use of pooled diet data may bias impact estimates given that prey such as squid, butterfish, and squid are more important diet items of older and larger bluefish. To address this potential bias, we performed a separate analysis to calculate bluefish consumption of prey using size or specific diet data (where available, see Morris[1]) as opposed to pooled data. The daily biomass of prey consumed by each age or size class (uncorrected for temperature) was calculated for the simulated population (a population with constant recruitment and mortality, see "Estimates of population consumption rate" section) and the 1995 bluefish population (a population whose biomass was dominated by older fish, see "Impact by age class" section and Table 1). These consumption-by-age estimates were multiplied by percent-contribution-by-weight data from Morris[1] for the four prey species described in the main analysis. The biomass of each prey type that was consumed was summed over all age classes to obtain the population consumption of each prey type. These values were then compared with values of population consumption of each prey type that were obtained by multiplying the total population consumption of all prey by the pooled prey contribution from Morris.

Results

Estimates of population consumption rate

The annual Q/B estimate from Pauly's (1986) model for the east coast bluefish population is 7.7. This means that the east coast bluefish population consumes a biomass of prey that is equivalent to ~8 times its own biomass over a one year period. The estimate of Q/B with Hartman and Brandt's (1995a) consumption-rate-at-weight data, adjusted for temperature, and estimated for the 1995 bluefish biomass on the U.S. east coast, was 10.8 (Table 1).

Impact by age class

For the simulated population with constant recruitment and mortality, the peak predatory impact of the bluefish population occurs between approximately age 1 and age 3 (Fig. 1). In 1984, a year with

fairly typical age structure, peak absolute consumption of prey occurred between age 2 and age 3 with a second peak at age 6 (Fig. 2). In 1995, when age structure was dominated by the 1989 year class, peak predatory impact occurred in fish that were six years of age (Table 1; Fig. 3). Therefore, much interannual variation in the age classes at which the peak predatory impact occurs should be expected in bluefish.

Comparison of biomass consumed by bluefish with that harvested by fisheries

The bluefish VPA biomass estimates from 1982 to 1995 ranged from a low of 124,024 metric tons (t) in 1995 to a high of 328,864 t in 1986 with an average stock size of 233,309 t for this period (NEFSC[3]). Given a Q/B estimate of 7.7, the minimum-size bluefish

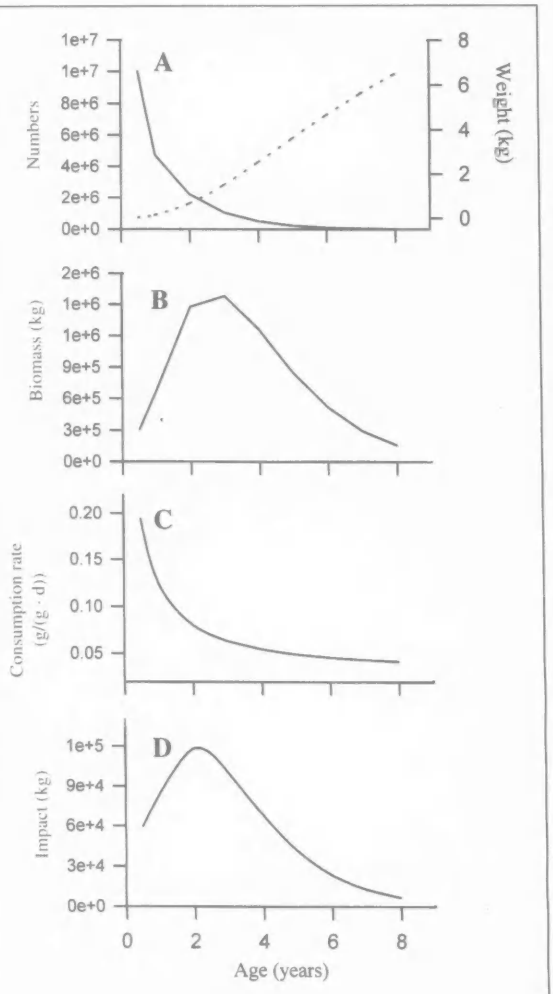

Figure 1

Estimates of bluefish impact on prey by age class for a simulated population of the U.S. east coast bluefish stock. Simulated numbers of bluefish (see text) and bluefish weight (kg; Wilk,1977) at age (**A**) were used to calculate bluefish biomass (**B**). Impact (kg) on prey by each age class (**D**) was calculated by multiplying bluefish biomass by maximum consumption rate (Hartman and Brandt, 1995a) for each age class (**C**).

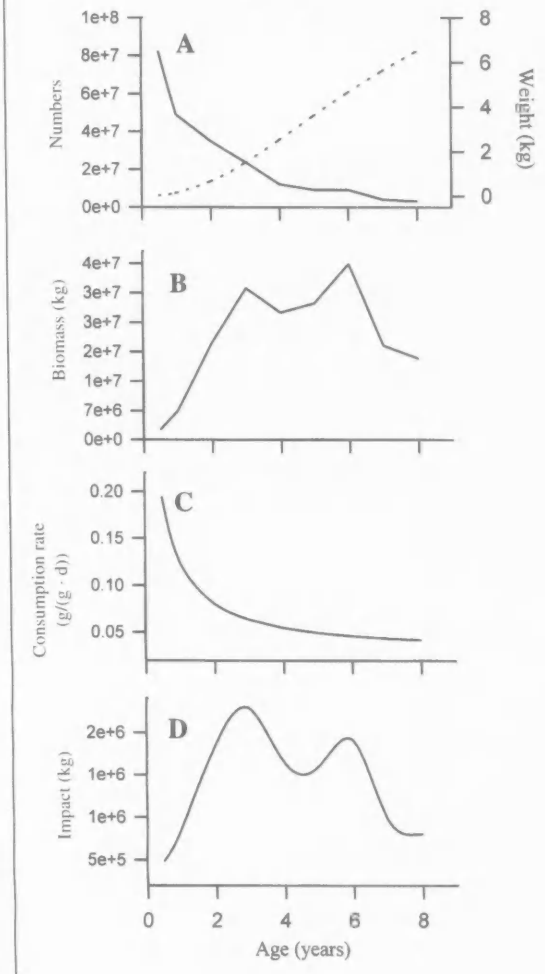

Figure 2

Estimates of bluefish impact on prey by age class for the U.S. east coast bluefish stock in 1984. Numbers of bluefish (NEFSC[3]) and bluefish weight (kg; Wilk, 1977) at age (**A**) were used to calculate bluefish biomass (**B**). Impact (kg) on prey by each age class (**D**) was calculated by multiplying bluefish biomass by the maximum consumption rate (Hartman and Brandt, 1995a) for each age class (**C**).

population (1995) consumed 0.9 million t per year whereas the maximum-size population (1986) consumed 2.5 million t of prey per year. The 1982 to 1995 average population biomass consumed 1.8 million t of prey per year.

Of the total biomass of prey consumed annually by bluefish, the fraction attributed to the primary resource species is an annual average of 10% butterfish, 10% long-finned squid, 5% boreal squid, and 5% Atlantic menhaden. These are also averages across bluefish body size; however, these averages may be too simplistic given that bluefish diet changes with increasing size. Much of the rest of the diet of bluefish is attributed to bay anchovy (described in Buckel et al., 1999a) for which no fishery landings exist. The average (minimum-maximum) annual consumption of butterfish by bluefish is therefore 90,000 t (48,000–125,000 t); annual consumtion of long-finned squid, is 90,000 t (48,000–125,000 t); and annual consumption of boreal squid, is 45,000 t (24,000–63,000 t). The annual consumption of these species by bluefish is much higher than the annual fisheries landings over the period 1984–92 (Fig. 4). The average consumption of Atlantic menhaden by bluefish was 45,000 t (24,000–63,000 t). The menhaden fishery takes seven times the biomass of menhaden that bluefish consume (Fig. 4).

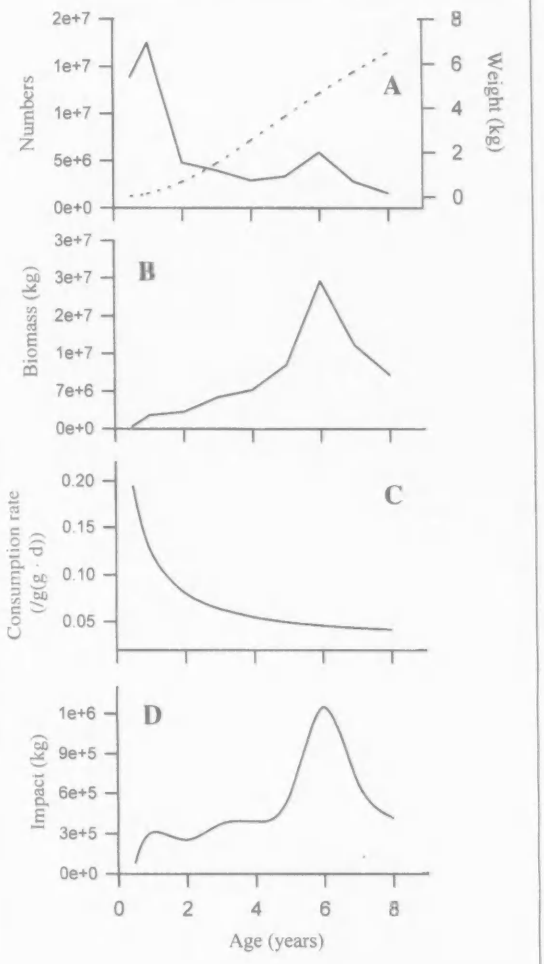

Figure 3

Estimates of bluefish impact on prey by age class for the U.S. east coast bluefish stock in 1995. Numbers of bluefish (NEFSC[3]) and bluefish weight (kg; Wilk, 1977) at age (**A**) were used to calculate bluefish biomass (**B**). Impact (kg) on prey by each age class (**D**) was calculated by multiplying bluefish biomass by maximum consumption rate (Hartman and Brandt 1995a) for each age class (**C**).

Effects of pooling diet across ages

For the simulated population, the daily consumption of long-finned squid and butterfish calculated by using age-specific data did not differ greatly from daily consumption when diets were pooled across ages (Fig. 5). However, the use of pooled diets overestimated daily consumption of boreal squid and Atlantic menhaden in comparison to values obtained with age-specific diets for both the simulated and 1995 bluefish population. For the 1995 population, age-specific diets gave daily consumption values for long-finned squid and butterfish that were higher than those that were calculated when pooled percent diet contributions were used (Fig. 5). Therefore, pooling diets can lead to under- or over-estimates of the predation pressure by bluefish; this bias can be affected by the age structure of the bluefish population.

Discussion

The results suggest that for at least three of the prey species of bluefish and humans, bluefish harvest a much higher biomass than does the fishery. This predatory loss will vary with fluctuations in bluefish abundance. We elaborate on management implications below.

Estimates of population consumption rate

Our estimate of Q/B (annual population consumption) is likely robust for two reasons. First, the estimate of bluefish annual Q/B is similar to that of other pelagic piscivores. Palomares and Pauly (1989) esti-

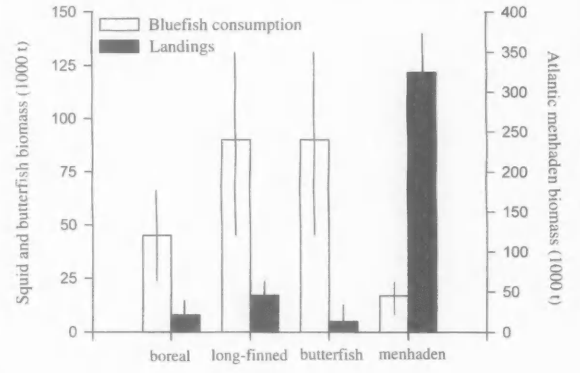

Figure 4

Estimated biomass (in thousands of metric tons (t)) of boreal squid, long-finned squid, butterfish, and Atlantic menhaden consumed by the U.S. east coast bluefish population (open histogram represents consumption by average bluefish biomass from 1982 to 1995, error bar represents range for consumption by a minimum to maximum bluefish population size) and harvested by east coast fisheries (closed histogram represents average harvest from 1984 to 1992, error bar represents range for harvest from minimum to maximum).

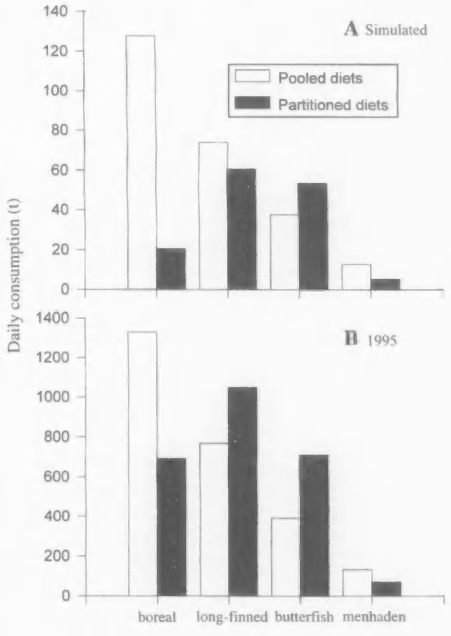

Figure 5

Daily consumption (not temperature corrected; t) of boreal squid, long-finned squid, butterfish, and Atlantic menhaden by the U.S. east coast bluefish population based on simulated (**A**) and 1995 (**B**) data (see text for calculation methods). Consumption was estimated from pooled diet indices (open histogram) and indices which were partitioned by age or size (closed histogram).

mated the annual Q/B of bar jack, *Caranx ruber*, and the dolphin *Coryphaena hippurus* at 10.6 and 8.5, respectively. Secondly, the estimate of Q/B with laboratory-measured daily rations (age 0–2 yr fish) and 1995 VPA bluefish biomass data gave us an estimate of Q/B of 10.8. This value was only slightly higher than the estimate from Pauly's (1986) model. This difference is likely a result of extrapolating C_{max} data from Hartman and Brandt (1995a) to larger fish. Assuming consumption rates of these larger fish were overestimated, values of 2.0 to 3.0 kg/(kg · d) · 100 were substituted for fish ages 4–9+. From this a Q/B value of 6.6 was estimated. This value is more similar to the Pauly model Q/B estimate of 7.7. Future estimates of bluefish population consumption should include laboratory or field estimates of feeding rates of older bluefish.

The Q/B estimate based on the 1995 VPA (10.8) incorporates the age structure existing at that time (recruitment not constant in the population), whereas the estimate from Pauly's (1986) model (7.7) assumes constant recruitment. Age structure may also contribute to the differences between the two Q/B estimates. For the 1995 bluefish stock, recent years of low recruitment have led to peak biomass in the older age classes (NEFSC[3]). These older, more abundant age classes consume a higher biomass of prey than younger age classes. In 1995, age-6 fish consumed more prey biomass than any other age class. This strong age class resulted from a relatively large recruitment in 1989. If recruitment and mortality are constant, our analyses predict that absolute prey consumption will peak at about age 2 (Fig. 1D). That consumption rate tends to peak in the earlier age classes has also been found in other species (Stewart and Binkowski, 1986; Yañez-Arancibia et al., 1993).

Bluefish ingest larger and a greater diversity of prey and include more resource species in their diet (e.g. butterfish, squid, Atlantic herring, and several groundfish species), with increasing body size (Buckel et al., 1999b; Morris[1]). When coupled with temporal shifts in the biomass age structure of bluefish, such ontogenetic changes in diet have important implications for impact on prey populations. For example, bluefish recruitment was relatively high from 1982 through 1984. In 1984, peak absolute consumption of prey occurred between age 2 and 3 compared with age 6 in 1995. In 1984, the biomass consumption of age-0 through age-3 fish was 40% of the entire

population's consumption, but it was only 18% of total population consumption in 1995 (Figs. 2 and 3). Similarly, Hartman and Brandt (1995b) found that relative prey consumption by bluefish at the population level in Chesapeake Bay varied with age structure.

The fact that age structure and ontogenetic diet shifts interact provides further justification for obtaining bluefish diet information by age or size. For example, the impact of the 1995 bluefish population on long-finned squid and butterfish was underestimated when pooled diet indices were used compared with diet indices that were partitioned by age or size (Fig. 5).

Comparison of biomass consumed by bluefish with that harvested by fisheries

Edwards and Bowman (1979) and Sissenwine et al. (1984) found that total piscivore consumption often exceeded fishery landings on Georges Bank. We have shown that bluefish alone consume an amount of squid and butterfish far exceeding the harvest of these species. How do our findings relate to the management of squid and butterfish? The current management plan for long-finned squid recommends a target yield of 21,000 t (Mid-Atlantic Fishery Management Council[5]). From calculations presented here bluefish consumed almost five times this amount of long-finned squid. Consistent with our findings, estimates of natural mortality for butterfish, long-finned squid, and boreal squid are high compared with other species (Anonymous, 1995; Atlantic butterfish, M=0.80; long-finned squid, monthly M=0.34; boreal squid, M>1.0). Our analysis does not allow us to determine what fraction of total prey mortality is due to bluefish consumption. Nor do we have estimates of impact of other predators on these prey. If we knew that bluefish were the dominant contributor to natural mortality in these prey, then questions regarding allocation could be dealt with more explicitly. For example, if the goal were to build larger squid stocks, would increased fishing mortality on bluefish be more or less effective than reductions in fishing mortality on squid? Future research should determine the magnitude of predation mortality resulting from bluefish and other predators. Until this information is available we must assume that predation mortality is similar to or below estimates of natural mortality for squid and butterfish. The management plan for these prey species assumes a high natural mortality (high predation mortality already taken into account) and fishing harvests are targeted accordingly.

However, these stock assessments assume that natural mortality is a fixed value. For prey of bluefish, this may not be true given the persistent changes in bluefish abundance on multiyear to decadal time scales. Natural mortality in squid and butterfish may vary greatly as a function of bluefish abundance. This has important management implications. For example, if bluefish abundance is high and remains so for extended periods and if this results in natural mortality rates on the prey that exceed the baseline natural mortality rates, then the biological reference points used in squid and butterfish management must be adjusted accordingly. Even if fishery removals are low in relation to those for other species, they may still contribute to population collapse by driving the prey population past the replacement level. Much more attention needs to be focused on assessment of the dynamics and predatory impact of bluefish if we wish to manage its prey, not to mention bluefish. Our results illustrate the importance of incorporating interspecific interactions in the management of marine fisheries (Sissenwine and Dann, 1991; Magnusson, 1995).

Bluefish may have limited influence on menhaden population dynamics because bluefish consumption of Atlantic menhaden was substantially below the fisheries landings of this species in our calculations. Oviatt (1977) estimated the aggregate demand for menhaden by bluefish in Narragansett Bay. She found that menhaden abundance was sufficient to meet the demands of bluefish even when the menhaden stock was low. Hartman and Brandt (1995b) found that combined predation by bluefish, weakfish, and striped bass on menhaden in Chesapeake Bay was low compared with fisheries harvest of menhaden.

There are several limitations to this analysis. The estimates of the biomass of prey consumed rely on several other estimated parameters. These include the VPA of bluefish biomass, the allometry of gross growth efficiency as a function of bluefish weight, diet estimates, and assumptions about the spatial and temporal location of the bluefish population. We therefore urge readers to view our estimates as rough approximations of the true values. At the very least, however, our analysis clearly suggests a need to greatly improve our knowledge of the population dynamics and foraging ecology of bluefish. In particular, more accurate data on bluefish abundance, spatial distribution, and diet as a function of bluefish size, season of the year, and habitat (e.g. estuary, coastal shoreline, or offshore) are required.

[5] Mid-Atlantic Fisheries Management Council. 1996. Amendment 6 to the fishery management plan and the draft environmental assessment for the Atlantic mackerel, squid, and butterfish fisheries. [Available from Mid-Atlantic Fishery Management Council, Room 2115, Federal Building, 300 South New Street, Dover, DE 19904-]6790, 16 p.]

For example, it has been shown that pooling bluefish diet by age or size class may over- or under-estimate the impact of bluefish compared with estimates of impact obtained when using age or size partitioned diets. Additionally, the diet of bluefish in estuaries (Oviatt, 1977; Hartman and Brandt, 1995c; Buckel et al., 1999a), where YOY bluefish are known to be dominant piscivores, was not considered here. Buckel et al. (1999a) showed that YOY bluefish in the Hudson River estuary are key predators on YOY striped bass and that recruitment success of striped bass is negatively correlated with YOY bluefish abundance. In the Chesapeake Bay, the percentage of menhaden in bluefish diet can be over 80% of the diet by weight (Hartman and Brandt, 1995c), much higher than the diet proportion we used in our analyses. A synoptic study examining the diet on the shelf and estuarine environments, as well as temporal and spatial distributions, will be required to determine the exact proportions of prey items in the coastal bluefish population.

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Sidescan-sonar mapping of benthic trawl marks on the shelf and slope off Eureka, California

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Abstract.—The abundance and orientation of trawl marks was quantified over an extensive portion (>2700 km^2) of the Eureka, California, outer shelf and slope, an important commercial bottom trawling ground for such high-value species as rockfish, sole, and sablefish. Fishing logbook data indicate that the entire reporting area was trawled about one and a half times on an average annual basis and that some areas were trawled over three times annually. High-resolution sidescan-sonar images of the study area revealed deep gouges on the seafloor, caused by heavy steel trawl doors that act to weigh down and spread open the bottom trawls. These trawl marks are commonly oriented parallel to bathymetric contours and many could be traced for several kilometers. Trawl marks showed a quadratic relationship in relation to water depth, with the greatest number of trawl marks observed at ~400 m. There was a significant positive correlation between the number of trawl marks observed on the sidescan images and the number of annual trawl hours logged within reporting areas. This finding indicates that acoustic remote sensing is a promising independent approach to evaluate fishing effort on a scale consistent with commercial fishing activities. Bottom trawling gear is known to modify seafloor habitats by altering benthic habitat complexity and by removing or damaging infauna and sessile organisms. Identifying the extent of trawling in these areas may help determine the effects of this type of fishing gear on the benthos and develop indices of habitat disturbance caused by fishing activities.

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Concerns about trawl impacts on benthic fish habitats date back to the earliest use of this gear in the 13th and 14th centuries (de Groot, 1984), but the extent and longevity of these impacts have been difficult to quantify. The effects of trawling depend on the size and type of bottom trawl, footrope gear, bridles, doors, scope of main wires, trawling speed, duration, and repetition of trawling. Vulnerability of the sea floor to trawling impacts depends on the nature of the bottom type, benthic fauna, sedimentation rates, tidal velocity, and the degree of reworking of sediments caused by storms. Seabed disturbance can occur over the entire distance between the doors but is most pronounced in the region scoured by the trawl doors (Messieh et al., 1991), which have been shown to plough to depths greater than 15 cm (Caddy, 1973; Churchill, 1989).

In the short term, disturbance from bottom trawling can cause resuspension of sediments and make benthic infauna more available to scavenging predators (Kaiser and Spencer, 1994; Kaiser and Ramsay, 1997; Ramsay et al., 1997; Lindeboom and de Groot, 1998). Long-term shifts in abundance and

diversity of benthic fauna have been noted in areas where trawling has been conducted for extended periods of time (Reise, 1982; de Groot, 1984; Sainsbury, 1987; Hutchings, 1990; Collie et al., 1997; Lindeboom and de Groot, 1998). Chronic, long-term disturbance can delay or prevent recovery of ecological communities (Collie et al., 1997) and large-scale removal of macrobenthos can lead to permanent changes in the community (Jones, 1992; Collie, 1998; Rogers et al., 1998). The removal of benthic organisms and sedimentary structures (e.g. sand waves, depressions) by trawls can lead to modifications of the physical complexity of benthic habitats (Reise, 1982; Jones 1992; Auster et al., 1996; Collie, 1998; Dorsey and Pederson, 1998). Schwinghamer et al. (1996, 1998) found that trawling homogenized sediments on the Grand Banks of Newfoundland to a depth of at least 4.5 cm, thus reducing fine-scale complexity of the substrate. Sediment mixing and frequent bottom disturbance from trawling activity may affect resuspension fluxes and produce changes in the successional organization of soft-sediment infaunal communities (Pilskaln et al., 1998). Reduction or removal of benthic structural complexity can lead to reduced recruitment of benthic organisms and often to reduced production (Botsford et al., 1997).

The degree of impact on benthic habitat is related to the timing, severity, and frequency of disturbance (Watling and Norse, 1998). The average annual area swept by trawls on Georges Bank from 1976 to 1991 was between 200% and 400% of the total area (Auster et al., 1996). Trawling does not occur evenly over this area but is concentrated in locations that produce better catches and fewer obstructions to towing (Dorsey and Pederson, 1998; Auster and Langton, 1999). As a result, some areas are subjected to trawling at a much higher rate than these reported averages and other areas may not be trawled at all. The effects of dredging on tidal flats in the Wadden Sea persisted for more than 15 years (van der Veer et al., 1985); by contrast, experimental trawl marks in a relatively dynamic intertidal zone in the Bay of Fundy persisted only 2–7 months (Brylinsky et al., 1994). The effects of mobile fishing gear on biodiversity are most severe where natural disturbance is least prevalent, such as at outer continental shelf and slope habitats (Watling and Norse, 1998). An experimental program to examine the impacts of mobile fishing gear on the benthic ecosystems in Atlantic Canada clearly indicated that trawling changed the physical habitat structure on sandy bottom at 120–146 m over a three-year period (Gordon et al., 1998). Biomass of epibenthic organisms in the trawl catch decreased with repeated trawling and the total biomass, as sampled by epibenthic sled, was lower in trawled areas compared with adjacent habitats. Fishing effort is spatially nonuniform, and thus techniques are needed that will allow analysis of trawling activity, and thus trawling impacts, on spatial scales appropriate to the large scales on which fisheries operate. In this study, we examine sidescan-sonar records as one approach to this analysis.

The continental shelf off Eureka (water depths less than ~120 m) is relatively flat (<0.5 degree) and topographically very smooth due to large inputs of fine terrigenous sediments from the Eel and Mad Rivers and reworking by storms (Fig. 1; Goff et al., 1999). Bottom photographs and samples from the shelf generally show smooth, mud-covered bottom with small-scale bottom roughness resulting from bioturbation and occasional wave ripples (Wiberg et al., 1996). The dominant morphological feature of the shelf is the Eel River delta, a sediment bulge in water depths of 20 to 60 m adjacent to the mouth of the Eel River and elongated to the north. Slope deposits are dominated by fine-grain sediments that show a transition from sandy silt in the south near the Eel Canyon to clayey silt in the northern portion of the study area (Syvitski et al., 1996).

Seafloor depressions 5 to 20 m in diameter and several meters deep, termed "pock marks," are common on both the outer shelf and slope throughout the region. These depressions are inferred to form by the removal of particles during expulsion of gas and fluid from subsurface deposits (Yun et al., 1999). The excavation is thought to occur both at slow rates, inducing particle-by-particle removal, and at rapid rates during sudden release of subsurface gas by earthquake shaking or other mechanisms (Field and Jennings, 1987).

In addition to natural processes that modify the seafloor, such as bottom currents, landslides, and fluid-expulsion features, the sidescan data and bottom photographs also show evidence (trawl marks) of fishing activities that modify these benthic habitats. The northern California outer continental shelf and slope off Eureka are important commercial fishing grounds. The trawl fleet that fishes the area off Eureka presently consists of 36 vessels from Eureka and 29 from Crescent City.[1] These vessels range in size from 18 to 24 m (60 to 80 ft), the larger vessels having entered the fleet in recent years in response to a shift of fishing effort into deeper water. Trawl designs vary but currently the most common trawl configuration is a Nor'eastern design with 114-mm (4 1/2 in) diamond stretched-mesh polyethylene netting equipped with roller gear. Trawls are currently

[1] Quirollo, L. F. 1998. California Department of Fish and Game, 619 Second Street, Eureka, CA 95501. Personal commun.

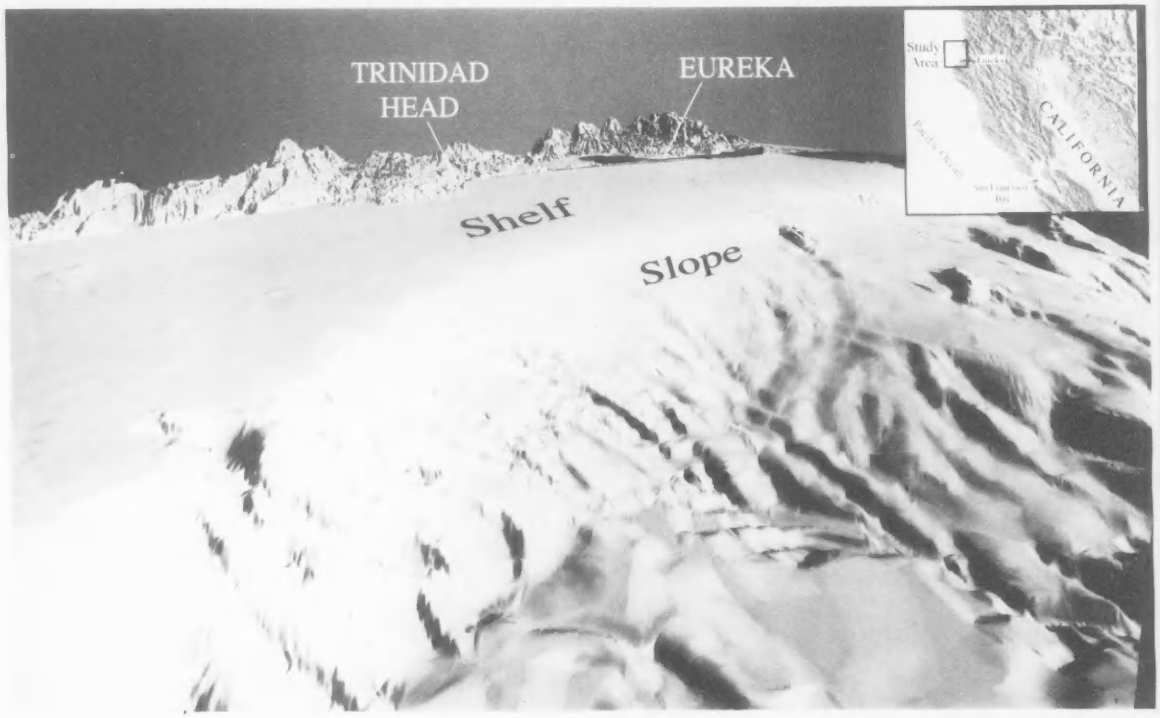

Figure 1

Perspective, shaded-relief view of the study area based on high-resolution multibeam bathymetry. Vertical exaggeration is 20×. The continental shelf (<120 m water depth) is bathymetrically smooth owing to large input of fine terrigenous sediments from the Eel and Mad Rivers and to reworking by storms. The southern portion of the shelf is dominated by the Humboldt slide. The northern portion of the slope is ~60 m deeper and ~7 km farther from shore than in the Humboldt slide area.

rigged with a 33.5-m (110-ft) net opening with trawl doors hung ~76–91 m (250–300 ft) apart.

The trawl fishery on the shelf primarily occurs over soft-sediment habitat and mainly targets flatfishes. The important species in this assemblage include English sole (*Pleuronectes vetulus*), Petrale sole (*Eopsetta jordani*), and sanddabs (*Citharichthys* spp.). The slope fishery occurs over rougher and more heterogeneous habitats that begin at the shelf break (~120 m) and continue to depths >900 m. The catch in this assemblage is dominated by Dover sole (*Microstomus pacificus*), sablefish (*Anoplopoma fimbria*), thornyheads (*Sebastolobus* spp.), and several rockfish species (*Sebastes* spp.). A midwater trawl fishery also exists in waters above the slope for Pacific whiting (*Merluccius productus*) and widow rockfish (*Sebastes entomelas*). The assemblages in this region are similar to those found along other portions of the U.S. west coast by the National Marine Fisheries Service triennial trawl surveys (Jay, 1996).

Groundfish are among the most diverse and economically valuable fishery resources along the west coast of the United States (NOAA, 1996). Diversity, quality, and extent of habitat are among the most important environmental determinants of distribution, abundance, and species diversity for groundfish (Carlson and Straty, 1981; Matthews and Richards, 1991). The broad spatial extent of these fisheries generally precludes careful examination of the nature of the exploited habitats, the relationship among species and habitats, and the degree to which fishing activities have affected these habitats. Conservation of fisheries habitat is an important consideration for sustaining fisheries production. The reauthorization of the Magnuson-Stevens Fisheries Conservation and Management Act requires incorporating the concept of "essential fish habitat" in Fishery Management Plans (Schmitten, 1996). Because fishing, particularly with bottom trawls, can alter essential fish habitat, it is important to quantify fishing activity and its effects on the associated habitat. The goals of this study are to evaluate the extent of marks from bottom trawls off Eureka, California, at a scale consistent with commercial fishing

activities and to compare these results with fishing-effort data from commercial fishery logbook data.

Materials and methods

Geological setting

The study area is the upper continental margin of northern California, north of Cape Mendocino. The shelf and slope in this region are within the Eel River Basin, a forearc basin filled with sediment derived from high sediment loads during the late Neogene (Clarke, 1992). The entire basin is highly faulted and folded from multiple episodes of deformation. Shearing and compression of the margin related to underthrusting of the Gorda plate beneath the North American plate has resulted in thrust faulting, uplift, and an overall youthful geologic setting, and this has produced varied relief and structure of the seafloor (Carver, 1987; Clarke and Field, 1989).

Studies of seafloor structure and sediment history of this area (Field et al., 1999; Gardner et al., 1999; Goff et al., 1999) have identified many features related to submarine landslides and to downslope sediment transport through channels and gulleys. Sidescan-sonar images of the seafloor along the shelf and slope, as well as multibeam maps, high-resolution seismic reflection data, and instrumented tripods from complementary investigations, all show abundant evidence of modern processes at work on the seafloor (Field and Jennings, 1987; Alexander and Simoneau, 1999; Field et al., 1999; Gardner et al., 1999; Goff et al., 1999; Yun et al., 1999).

There are three main types of relief on the seafloor in this region. Along the slope, in the center of the study area, a large growth fold (anticline) has uplifted through the modern seafloor, exhibiting 100 m of steep relief. South of the anticline, the slope between 120 and 600 m depths is dominated by the Humboldt slide, an area where slope deposits have undergone deformation and limited downslope movement (Field and Barber, 1993; Gardner et al., 1999). North of the anticline, the slope is crossed by a series of shallow gullies that are 100 to 200 m wide and 1 to 2 m deep (Field et al., 1999). Gullies are spaced about 200 to 300 m apart. Gullies also occur south of the anticline where they are generally fewer in number and somewhat deeper (~20 m). The gullies are thought to represent sediment pathways during earlier periods when sea level was at a lower position.

Sidescan survey

Through a collaborative effort of the U.S. Geological Survey (USGS) and the National Marine Fisheries Service (NMFS), we examined sidescan-sonar data off Eureka, California, collected by the USGS during the STRATA FORMation on Margins (STRATAFORM) program sponsored by the Office of Naval Research (Nittrouer and Kravitz, 1996; Nittrouer, 1999). A grid of 1600 line kilometers of high-resolution, digital, deep-towed (95 kHz) sidescan-sonar data was obtained during 1995 and 1996 (Fig. 2). The sidescan-sonar images were obtained by using the USGS Datasonics SIS-1000 chirp sonar system and an ISIS data-acquisition system. The sidescan sonar operates as a swept FM signal with a frequency band from 90 to 110 kHz (port channel sweeps from low to high, starboard channel sweeps high to low). Usual swath width during the cruises was 0.5 s (750-m swath). Sidescan data were recorded on magneto-optical disks and downloaded to a DEC ALPHA workstation. The digital sidescan-sonar data were all processed with USGS MIPS image-processing software (Chavez, 1984; 1986). The raw data were geometrically corrected (slant range) by using the position, heading, speed, and nadir depth of the ship. Each of the 8-bit image pixels was geometrically located by assuming a flat seafloor which introduces a certain amount of uncertainty into the actual location of any given pixel. Our estimated location accuracy was about 100 m. After the geometric corrections were made, anamorphic corrections were applied to account for the aspect ratio between along- and across-track directions. Radiometric corrections had to be applied to the 8-bit digital number (DN) that represents backscatter. Each sidescan line was subdivided into segments and, for each segment, the average DN for each binned range was normalized to the mean of all the binned ranges within that segment. Each segment was several hours long, and this correction produced tone-matched adjacent segments.

Trawl marks

Trawl marks appear on the sidescan sonographs as long, narrow, linear depressions (Fig. 3). Trawl marks were traced on mylar overlaid on the sidescan records. Each sidescan track line was divided into 10-min time intervals. Vessel speeds during the surveys varied between 3 and 4 knots, and therefore each 10-minute interval covered from 0.9 to 1.2 km along the ship's course. The sidescan record covered a 750-m swath so that 10-min segments represent from 675,000 m^2 to 900,000 m^2 of area. To quantify the number of trawl marks per time interval, lines were drawn perpendicular to the course of the sidescan track line, and trawl marks that bisected these lines were counted. Mean trawl mark length was 0.77 km (SD=0.26) for 20 randomly selected 10-min

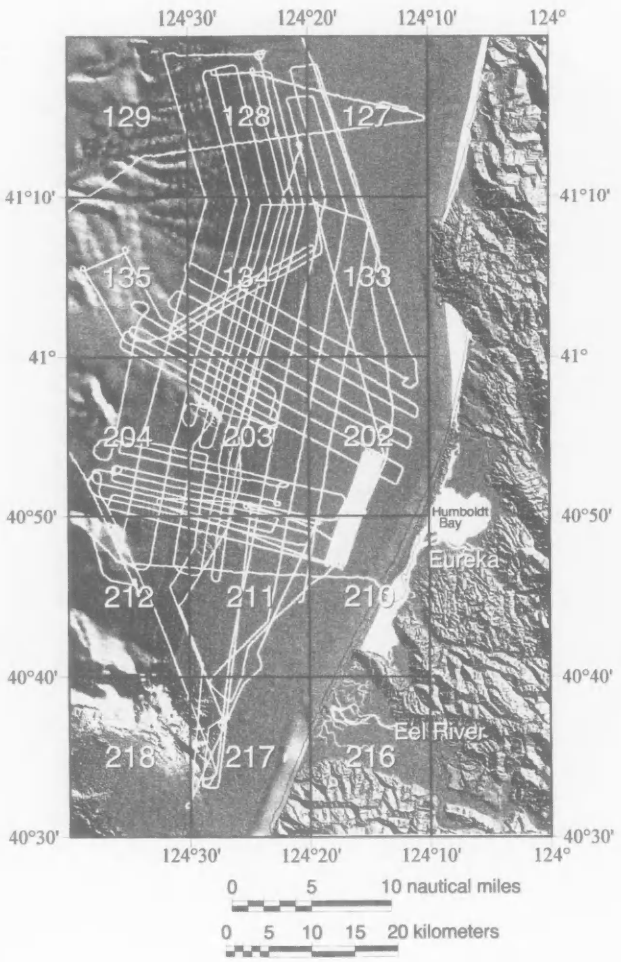

Figure 2

Track lines for high-resolution sidescan-sonar surveys. The reporting blocks from California Department of Fish and Game that are used for logbook data entry are superimposed on the survey area. Blocks are 10 minutes of longitude and 10 minutes of latitude on a side with block number in the center.

intervals from 10 different sidescan track lines (Fig. 4). From these results, it was determined that two random perpendicular lines were needed to properly sample each 10-min interval and minimize double-counting of trawl marks. Using a sample of 50 randomly selected 10-min time intervals from 10 sidescan track lines, we counted the actual number of trawl marks and compared this number with the mean number counted with the perpendicular line intercept method described above. The mean proportion of trawl marks counted with this sampling method to actual number of marks was 0.84 (SD=0.11). Trawl mark density in km^2 was calculated from each time interval and incorporated into a Geographical Information System (GIS) for analysis and contouring.

The angle of each trawl mark was measured in relation to the two perpendicular lines used to quantify trawl marks in all 10-min intervals. These angles were adjusted for the course of the sidescan track and computed in relation to magnetic north. Mean angles for each time interval were then calculated and plotted on a polar plot in an $r = f(\theta)$ format, where r is the number of trawl marks and theta (θ) is the angle relative to 0°. The grand mean angle and 95% CI were computed with the mean values from each time interval (Zar, 1984).

Fishing effort

Trawlers provide information on catch and effort of individual trawl hauls to the California Department of Fish and Game (CDF&G). Hauls are spatially recorded in blocks that are 10 minutes of latitude by 10 minutes of longitude (Fig. 2). Blocks within the Eureka STRATAFORM survey area were extracted from the NMFS Tiburon Laboratory groundfish database and used in these analyses. Trawling is prohibited by state law within 5.6 km (3 nm) of the coast. All reporting blocks adjacent to the coast were truncated for all estimates and comparisons.

Pacific whiting form extensive midwater aggregations during the day, and the fishery is conducted almost exclusively with midwater trawls (Dorn and Saunders, 1997). Because fishermen did not report whether their trawl hauls were bottom trawls or midwater trawls, all trawl hauls with catches of Pacific whiting greater than 454 kg (~1000 lb) were eliminated from these analyses. Mean annual fishing effort (trawl hours) was calculated for each reporting block within the Eureka area for the years 1990 to 1994. Depths from the logbook data were used to obtain mean fishing depths for each reporting block for comparisons with fishing effort.

The reporting block grid was incorporated into a GIS and the mean density of trawl marks was calculated for each block (Table 1). Water depths from a high-resolution multibeam mapping survey (Goff et al., 1999) were binned to obtain mean bottom depth in each block for comparison with mean number of trawl marks. Effort, expressed as mean annual trawl

hours per block, was compared to the mean number of trawl marks in each reporting block with a Spearman rank order correlation. Two reporting blocks (129 and 218) were excluded from this analysis owing to a lack of adequate sidescan coverage. To estimate the total area swept by bottom trawls on an annual basis, the total annual number of fishing hours per reporting block was multiplied by a typical vessel speed (5.5 km/h) and a typical door to door width of 85 m.

Detrended correspondence analysis (DCA) was used to identify clusters of similar reporting blocks in ordination space on the basis of fish assemblage structure from CDF&G logbook data (Ludwig and Reynolds, 1988). A matrix of reporting blocks by catch was created for use in this analysis. Habitat types were defined *a priori* by depth and physical characteristics of the habitat from previous geological surveys and then overlaid on the station clusters created by DCA. A Kruskal-Wallis rank sum test (Hollander and Wolfe, 1973) was used to compare the density of trawl marks and total fishing hours per reporting block in each habitat type discerned by DCA. Pairwise comparisons of trawl marks and fishing effort between habitats was conducted by using Dunn's multiple comparison procedure at $\alpha = 0.05$ (Hollander and Wolfe, 1973).

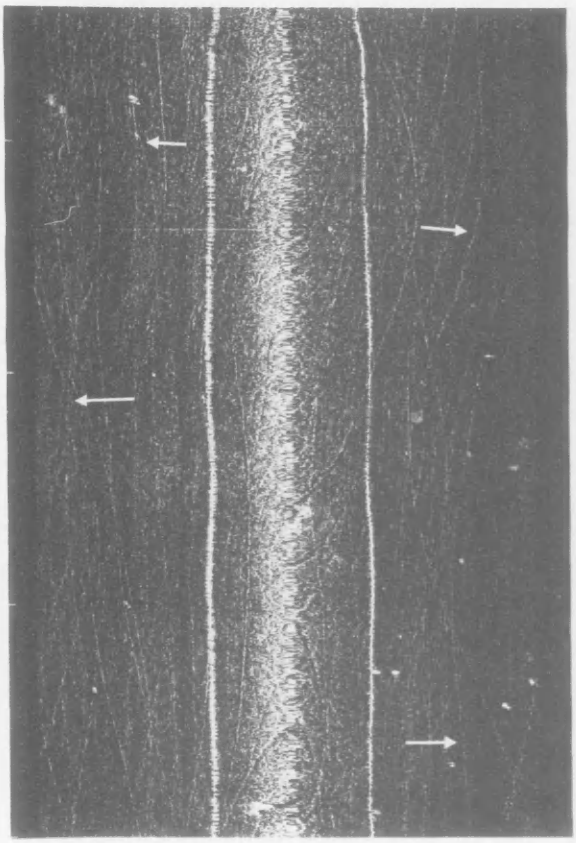

Figure 3

Sidescan-sonar image (white is shadow; dark is reflection) of trawl marks on the seafloor at a water depth of ~150 m. Sidescan swath width is 750 m. Tick marks are 5-min time intervals (~0.55 km). Arrows point to examples of trawl marks. Shallow circular depressions on the sonograph are gas pockmarks. Ship's course for this sonogram is 345°.

Results

We measured the range, density, and orientation of marks on the seafloor caused by trawling activity as resolved by the sidescan-sonar records. Of the 1246 10-min intervals examined, ~10% were washed out and could not be analyzed. Densities of trawl marks/km^2 per 10-min interval ranged from 0.00 to 98.55 and mean density per block ranged from 0.94 to 38.3 with a grand mean of 20.0 marks/km^2 (Table 1). Trawl marks were most abundant on the slope, particularly the northern portion and least abundant on the continental shelf (Fig. 5).

Trawl marks commonly were oriented parallel to isobaths and some could be traced for several km (Fig. 6). The overall mean trawl direction was 352.6° (95% CI +/–5°) (Fig. 7) which agrees with the general orientation of isobaths in this area. Because trawl marks were generally orientated in the north–south direction along isobaths, sidescan tracks orientated in the east–west direction (>45° and <135°) might not distinguish as many trawl marks in relation to those orientated in the north–south direction. Using 25 randomly selected time intervals from five east-west sidescan track lines and 25 from five north–south track lines, we found that the proportion of trawl marks sampled with the perpendicular line intercept method was not significantly different from the actual number of trawl marks for the two track line orientations (Mann-Whitney rank sum test=759.5, P=0.775).

We compared the orientation of trawl mark angles between east–west and north–south orientations by selecting seven locations where east–west and north–south sidescan-sonar track lines intersected during the 1996 survey. The intersecting time interval, along

with one time interval to either side were pooled for each orientation (21 time intervals for each orientation) and compared by using a Watson-Williams two-sample test for mean angles (Zar, 1984). There was a significant difference (F=44.7, P<0.001) in the mean angle of trawl marks detected along north–south orientated track lines (mean=357.9) compared with east–west orientated track lines (mean=294.5) at these intersection points.

The mean density of trawl marks in each CDF&G reporting block fitted a quadratic relationship with water depth ($y=-0.0002x^2 + 0.1374x + 2.9353$, R^2=0.501, P=0.04). The lowest density of trawl marks was observed in the shallowest water with maximum number of trawl marks observed at ~400m depth (Fig. 8). Mean annual trawl hours (1990–94) also fitted a quadratic model with water depth for each reporting block ($y=-0.0082x^2 + 8.7015x - 960.57$, R^2=0.723, P<0.001) (Fig. 8). There was a significant positive correlation between the density of trawl marks and the mean annual number of trawl hours per reporting block (r_s=0.573, P=0.048).

The fishing blocks off Eureka can be separated into three depth zones on the basis of fish assemblages analyzed by DCA (Fig. 9). The upper and mid slope blocks are relatively close in DCA ordination space, whereas the shelf blocks showed a distinct assemblage structure. The shelf blocks nearest the coastline have effective fishing depths of ≤102 m (Table 2). From logbook data, the dominant species at these depths are flatfishes (e.g. sanddabs, Petrale sole, and English sole) and rockfishes. Dominant species from trawling on the upper slope (175 to 437 m) primarily consisted of Dover sole and rockfishes. Thornyheads, Dover sole, and sablefish are the dominant species on the mid slope (effective fishing depth from ~595 to 837 m).

The mean density of trawl marks was significantly different (Kruskal-Wallis H=287.4, P<0.001) among the three depth zones recognized by DCA (Fig. 10A). Upper and mid slope depths were not significantly different from one another (P>0.05) but both had significantly greater numbers of observable trawl marks than the shelf depth zone (P<0.05). Mean annual fishing effort per block also showed significant differences among depths (Kruskal-Wallis H=9.5, P=0.009, Fig. 10B). Fishing effort was lowest in the shelf habitat and highest in the upper slope, although the upper slope and deep slope depth zones were not significantly different from one another (P>0.05).

The cumulative annual area swept by commercial bottom trawls, as calculated from logbook data, was compared to the total area in each reporting block (Fig. 11). The entire study area was trawled ~1.5 times on an average annual basis. The area trawled exceeded the total block area in the majority of the blocks. This

Table 1

Summary statistics for density estimates of trawl marks in each California Department of Fish and Game (CDF&G) reporting block. Block numbers with asterisks are excluded from comparative analysis with fishing effort owing to small sample size and lack of adequate block coverage.

CDF&G block	Mean (no/km²)	SD (no/km²)	Max (no/km²)	Min (no/km²)	n
127	25.22	16.77	52.92	0.00	34
128	35.07	18.56	98.55	2.09	132
129*	31.19	7.94	45.08	21.59	13
133	11.80	13.20	49.13	0.00	81
134	38.26	11.82	63.49	0.00	144
135	22.02	10.69	52.11	1.39	34
202	4.13	6.44	26.67	0.00	169
203	18.01	12.65	43.87	0.00	159
204	22.82	15.71	64.09	0.00	115
210	0.94	2.25	14.03	0.00	69
211	10.99	16.89	76.75	0.00	102
212	28.98	13.56	66.42	8.25	39
217	27.39	27.23	75.55	0.00	25
218*	28.68	15.58	39.69	17.66	2
Mean	19.99	18.34	98.55	0.00	Σ = 1118

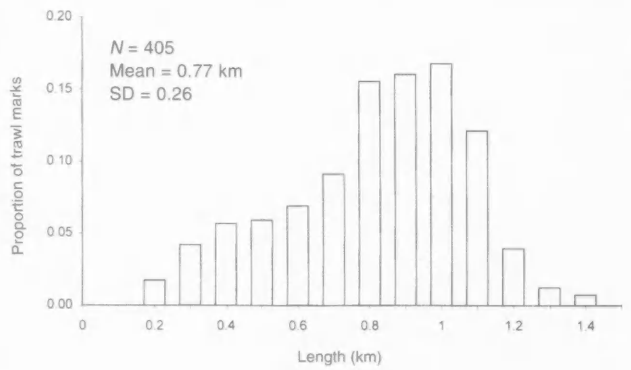

Figure 4

Frequency distribution of trawl-mark length per 10-min interval. Ten minute time intervals ranged from 0.77 to 1.2 km in length (mean=0.91). Data are from 20 randomly selected 10-min intervals from 10 different sidescan tracks.

was particularly true in the deeper blocks where the ratio of area trawled to block areas ranged from 127% to 339%.

The mean trawl depth and mean duration of hauls for bottom trawls off Eureka has increased steadily since the early 1980s (Fig. 12A). Along with this change in fishing depth has come a shift in the composition of species landed. Thornyheads are deeper-water species and their catch contribution has increased from ~4% of the total catch in the late 1970s to ~14% in the 1990s. Conversely, the English sole is a shallow-water flatfish whose landings have declined from nearly 7% of the total catch in the late 1970s to 2–3% in the 1990s.

Discussion

Utility of sidescan sonar

Acoustics are useful in fisheries for stock assessment (Karp, 1990), for remotely sensing characteristics of bottom habitat (Able et al., 1987; Greenstreet et al., 1997; Mayer et al., 1997; Yoklavich et al., 1997; Auster et al., 1998a, 1998b), and for assessing impacts to fisheries habitat (Auster et al., 1996; Collie et al., 1997). Our results demonstrate that the use of acoustic remote sensing also presents a promising independent approach for evaluating fishing effort on a spatial scale consistent with commercial fishing activities. Sidescan-sonar data are useful for identifying the location of trawling activity, as well as for evaluating the amount of disturbance to the seabed, and may be used in developing indices of habitat disturbance caused by fishing activities. Despite minimal sidescan coverage in some reporting blocks and biases in the logbook data associated with misreporting, there was a significant positive correlation between the density of trawl marks per reporting block from sidescan-sonar data and the mean annual number of trawl hours. A quadratic relationship with depth was observed for the number of trawl marks and fishing effort per reporting block with maximum values at ~400 m and ~500 m, respectively. This relationship, together with the density contour plot of trawl marks and the vector plot of trawl orientation, shows that fishing effort was concentrated on the upper to mid slope and along bathymetric contours.

The entire study area off Eureka is trawled ~1.5 times its total area on an annual basis. Because of narrow bands of rocky outcrops and anticlines, trawlable fishing area within the mid slope reporting blocks is less than the total area of the blocks. The area swept by trawls is therefore an under-estimate of the effective fishing area that is impacted by trawl gear in these blocks. Gislason (1994) estimated that trawling swept the entire area of the North Sea annually, with some fishing grounds in the southern North Sea likely being swept more than three times a year by beam trawls. This type of chronic impact on the seafloor can have a long-term effect on the local benthic epifauna (Rogers et al., 1998). For example, there is abundant evidence of rich ecological communities associated with cold-seeps and exten-

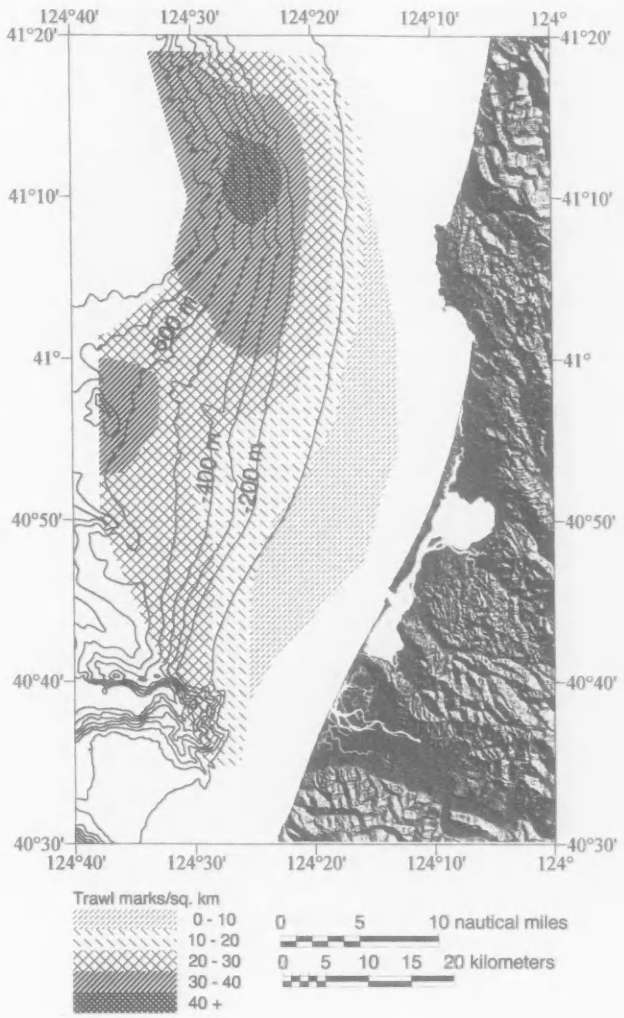

Figure 5

Contour plot of trawl mark densities (number/km²) derived from 10-minute intervals along sidescan survey track lines. Actual locations of data points are in Fig. 6.

sive bioturbation off Eureka (Syvitski et al., 1996). Released gases and fluids from cold seeps are rich in methane and sulfide and support unique productive cold-seep biological communities (Syvitski et al., 1996). The magnitude of trawling activity in this area has the potential to modify these communities by direct physical damage or by smothering from resuspended sedimention.

There has been increased interest in recent years on the impacts of fisheries on the marine environment (Dayton et al., 1995; Boehlert, 1996; Lindeboom and de Groot, 1998; Watling and Norse, 1998), and an important component is the relationship between exploited fish species and their associated habitats (Schmitten, 1996). With a greater understanding of these associations, concerns have been raised about the adverse impacts that mobile fishing gear may have on the entire ecosystem. The severity and duration of disturbance are both factors that affect ecological communities (Gislason, 1994; Connell et al., 1997; Tuck et al, 1998; Auster and Langton, 1999). Mobile fishing gear, such as trawls, is the most widespread form of direct disturbance to marine systems below depths affected by storms (Watling and Norse, 1998). Natural disturbances to the benthic community off Eureka probably occur from high-energy wave events, floods, and even tectonic activity. The first two processes likely have a greater impact in the shallower water on the shelf, and the latter process is likely too infrequent to play a major role in impacting the benthos. Thus, in the habitat covered by this study, trawls represent the greatest form of direct disturbance to the benthic habitat—a finding that is consistent with the conclusions of Watling and Norse (1998) for depths below the influence of storms. The extent and location of fishing activity, noted in this study from logbook data and sidescan-sonar records, can potentially have a large impact on the local ecological communities, particularly on the slope where the frequency and magnitude of natural disturbance is less than that on the shelf.

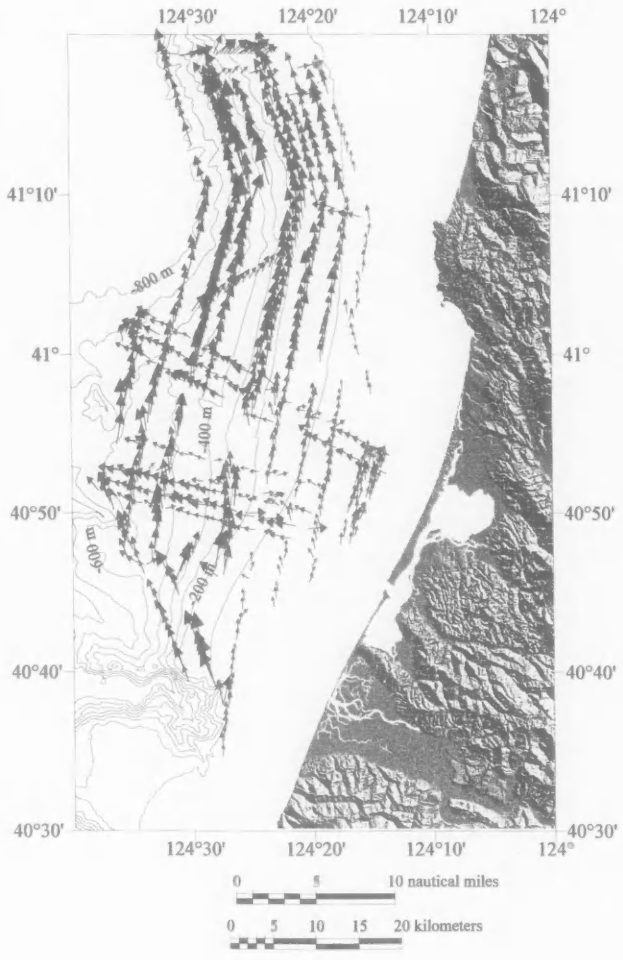

Figure 6

Vector plot showing orientation and magnitude of trawl marks along sidescan track lines. Length of arrow is proportional to the density of trawl marks in each 10-min interval, and direction is the mean angle of all trawl marks in each time interval. Note that angles are plotted in relation to north so that trawls towed north or south resulted in the same orientation.

Examination of trawl marks was not the primary goal of the sidescan-sonar survey conducted off Eureka (Syvitski et al., 1996). Consequently, there are aspects of the survey method that could have been conducted differently to improve the quality of these data. Because fishing activities in this area are generally conducted along the north–south bathymetric contours, sidescan-sonar tracks oriented east–west tended to resolve slightly fewer trawl marks. Any future study of trawl marks using sidescan sonar should concentrate tracks to orientations subparalleling trawling directions in order to maximize the resolution of the survey.

There are biases associated with this method, particularly in a dynamic physical location like the northern California continental margin. Estimates of the actual number of trawl marks are minimal because of variability in resolution of the sidescan records, obliteration of older trawl marks by more recent trawling, burial by sedimentation or reworking of the seafloor by

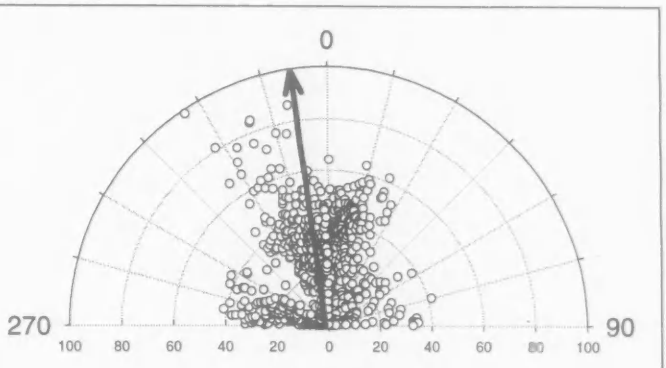

Figure 7

Polar plot of mean angle and density of trawl marks for each time interval. Polar plot in an $r = f(\theta)$ format where r is the density of trawl marks and theta (θ) is the angle relative to 0°. The grand mean trawl direction was 352.6° (95% CI +/–5°).

large waves, particularly at shallower depths. Trawl marks may persist for longer duration in deeper water where sedimentation rates are lower and storm waves have a lessened or negligible effect. Shelf sediment presently accumulates 2 to 10 times faster on the shelf than on the slope (1–3 mm/yr on the slope; 6–10 mm/yr on the shelf based on ^{210}PB activities; Alexander and Simoneau, 1999; Sommerfield and Nittrouer, 1999). At present rates, and assuming trawl track depths of ~15 cm, it would take 50–75 years to fill in a typical trawl mark, but evidence shows that small natural gullies on the slope are being draped and are infilled at present and thus maintain their shape and relief even though they are in the process of being buried (Field et al., 1999). The sedimentation rates on the shelf are higher than on the slope (the flood deposits from the 1964 Eel River flood now lies ~45 cm below the seafloor) (Sommerfield and Nittrouer, 1999), and annual storm waves resuspend sediments at depths up to 100 m. Resuspension and redeposition of silt particles may lead to draping of trawl gouges and thus preserve their shape and relief on the seafloor. In the presence of bottom currents, which usually are present from tides, storm waves, or boundary flows, the resuspended particles may fill in the trawl gouges and thus slowly erase them over time. Since fishing effort in the study area was shown to be concentrated in water deeper than 100 m, these effects are possibly compounded by the longevity of trawl marks in this habitat. Research is needed to address the longevity of trawl marks in various environments as well as to determine the impacts on (and recovery of) diversity and production in benthic communities.

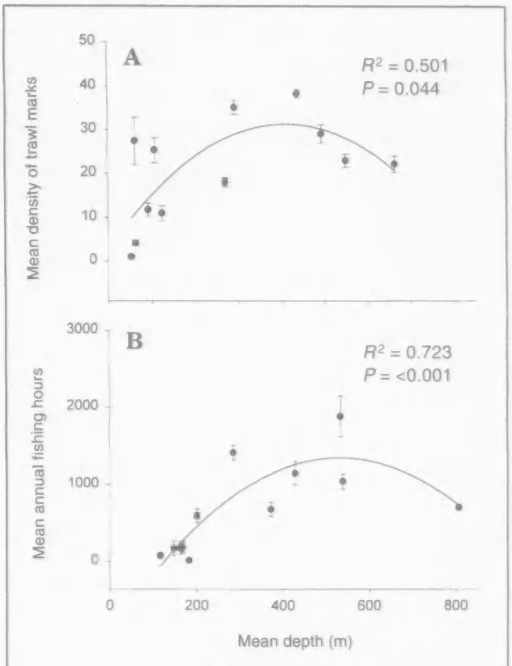

Figure 8

(**A**) The nonlinear relationship between mean density of trawl marks per 10-min interval by CDF&G reporting block depth (m). Mean trawl mark block depth is calculated from the mean depth of 10-min intervals along the sidescan track in each reporting block. (**B**) Mean annual fishing hours per reporting block and block depth (m). Mean fishing hour block depth is calculated from the depths reported from logbooks in each reporting block. Error bars are standard error of the mean.

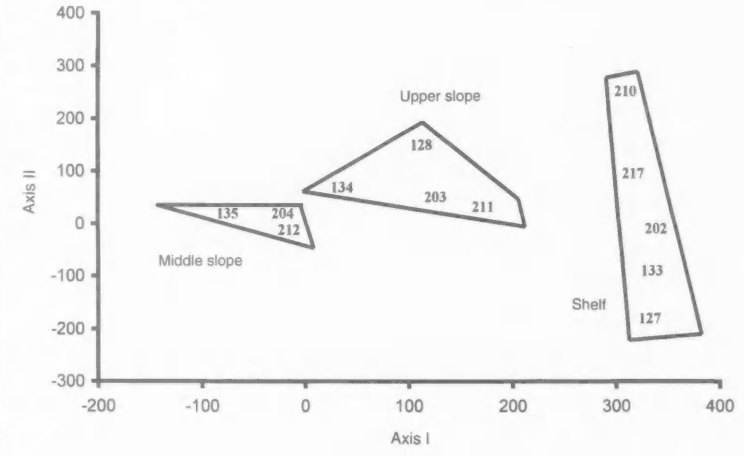

Figure 9

Results of a detrended correspondence analysis of mean annual species catch composition (1990–94) in CDF&G reporting blocks off Eureka. Three clusters are recognized as unique depth zones. Numbers are CDF&G reporting block numbers.

Table 2

Characteristics of California Department of Fish and Game (CDF&G) reporting blocks by habitat zone. Values for fishing depth are mean depth per trawl in each reporting block from logbook data (1990–94). Block depth and area are calculated from Geographical Information System (GIS) data and exclude areas within the 5.6-km (3-nmi) no trawl zone. Values for dominant species are percentages of mean total annual catch (1990–94).

Habitat zone	Block	Fishing depth (m)	Block depth (m)	Block area (km^2)	Fishing effort	Dominant species caught					
Shelf											
	127	68	83	251	191	Sanddab	30.31	English sole	27.59	Petrale sole	14.82
	133	102	83	207	16	Sanddab	33.31	English sole	14.35	Widow rockfish	9.87
	202	67	69	202	169	Sanddab	48.46	English sole	12.80	Petrale sole	11.88
	210	93	52	55	78	Rockfish	29.46	Sanddab	25.85	Petrale sole	14.25
	217	101	96	147	170	Widow rockfish	52.36	Rockfish	12.64	Sanddab	11.29
Zone mean		86	77	$\Sigma = 862$	$\Sigma = 623$	Sanddab	29.84	Rockfish	13.80	English sole	13.15
Upper slope											
	128	359	347	259	691	Dover sole	40.10	Rockfish	22.78	Sablefish	13.92
	134	437	425	259	1156	Dover sole	60.50	Sablefish	16.48	Thornyhead	7.76
	203	265	260	260	1425	Dover sole	34.07	Rockfish	21.41	Petrale sole	10.29
	211	175	118	256	599	Dover sole	22.68	Rockfish	22.52	Sanddab	13.49
Zone mean		309	288	$\Sigma = 1034$	$\Sigma = 3871$	Dover sole	39.34	Rockfish	10.18	Sablefish	10.95
Mid slope											
	135	837	873	259	707	Thornyhead	45.75	Dover sole	33.11	Sablefish	16.21
	204	539	583	260	1054	Dover sole	57.06	Sablefish	15.45	Thornyhead	12.13
	212	525	570	260	1900	Dover sole	51.92	Thornyhead	16.80	Sablefish	15.63
Zone mean		634	675	$\Sigma = 779$	$\Sigma = 3661$	Dover sole	47.36	Thornyhead	24.89	Sablefish	15.76

The general temporal trend in fisheries development begins with localized fisheries that then expand geographically and to less accessible habitats, such as the deep sea (Deimling and Liss, 1994). In the present study, mean trawl depths have increased over the years as a result of changes in management strategies, changes in market demands, and overfishing of nearshore resources. Shortspine thornyheads (*Sebastolobus alascanus*) and longspine thornyheads (*S. altivelis*) are slope rockfish species whose landings have increased along the West Coast in recent years (Ianelli et al., 1994) whereas English sole has decreased. An export market for thornyheads developed during the 1980s because a similar and highly valued species (*S. macrochir*) was depleted off Japan (Rogers et al., 1997). As the Japanese market developed, the trawl fishery moved into deeper water following a typical pattern (Deimling and Liss, 1994) where longspine thornyheads and larger shortspine thornyheads are most common. Several of the most important species in the trawl catch (e.g. Dover sole and sablefish) segregate at depth by sex, size, and maturity stage. These biological characteristics as well as size and harvest restrictions makes interpretation of changes in the catch of these species difficult to interpret.

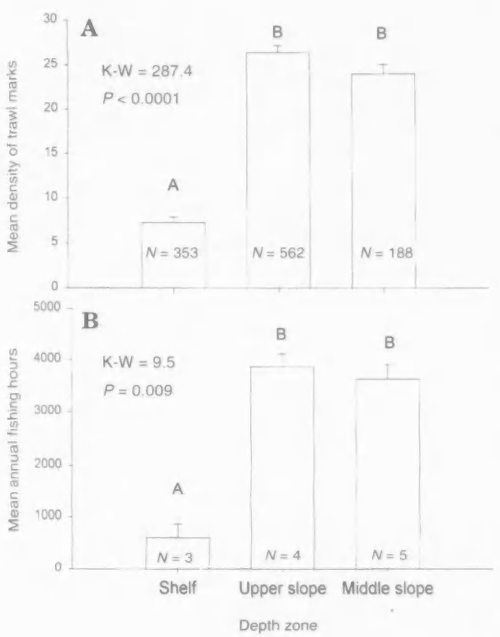

Figure 10

(**A**) Mean density of trawl marks per 10-min interval for the three habitat zones recognized by DCA. N = the number of time intervals in each habitat zone. (**B**) Mean annual fishing hours per CDF&G reporting block for the three habitat zones recognized by DCA. N = the number of reporting blocks in each habitat zone. Error bars are standard error of the mean. Statistical results from Kruskal-Wallis rank sum test. Dunn's multiple comparison procedure, $\alpha = 0.05$. Habitats with the same letter designation are not significantly different from one another.

Implications for management

The groundfish trawl fishery has experienced declining catches and increasing regulation in recent years. Current management strategies are imposed primarily on individual species or among small groups of congeneric species. These strategies do not address the impact to essential fish habitat from fishing activities and therefore may not be appropriate for the long-term sustainability of these resources. Marine reserves or harvest refugia are an effective management strategy that can help protect and maintain the complexity and quality of fish habitat as well as mitigate the direct effects of fishing (Bohnsack, 1996; Bohnsack and Ault, 1996; Auster and Shackell, 1997; Yoklavich, 1998). A number of studies have noted reduced diversity and abundance of emergent epifauna in trawled areas compared with adjacent areas closed to fishing (Bradstock and Gordon, 1983; Auster et al., 1996). The demersal trawl fishery off northwest Australia was thought to be responsible for a significant loss of emergent epifauna and decreased fish productivity (Sainsbury, 1987, 1988), both of which recovered in an area closed to fishing. The establishment of harvest refugia may be the most effective method of reducing the impact of trawls to benthic habitat and subsequently may help to improve the sustainability of the associated fish assemblages.

Detailed analysis of sidescan-sonar data has allowed us to map and quantify trawl marks in relation to fishery and habitat distributions. The combination of geophysical data with fisheries dependent and independent data in a GIS provides the ability to examine the impact of trawling at a scale appropriate for fisheries management. Evaluation of benthic habitat disturbance caused by fishing activities is important for meeting the mandate of the Sustainable Fisheries Act. Developing indices of benthic habitat disturbance can be valuable in comparing the impact of fishing activities among different areas and in establishing baselines for evaluating future management strategies such as closed areas.

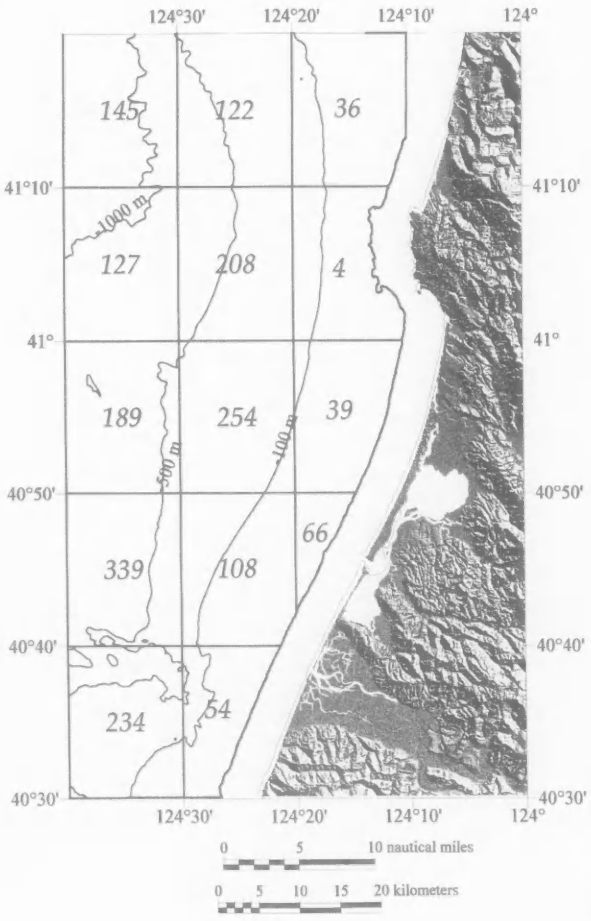

Figure 11

Total area trawled within each reporting block as a percentage of the total block area. Area trawled was calculated from the product of mean annual fishing effort (1990–94) from logbook data, typical vessel speed (5.5 km/h), and a typical trawl door to trawl door width of 85 m. "No trawl" areas within 5.6 km (3 nmi) of shore are not included in the total area calculations.

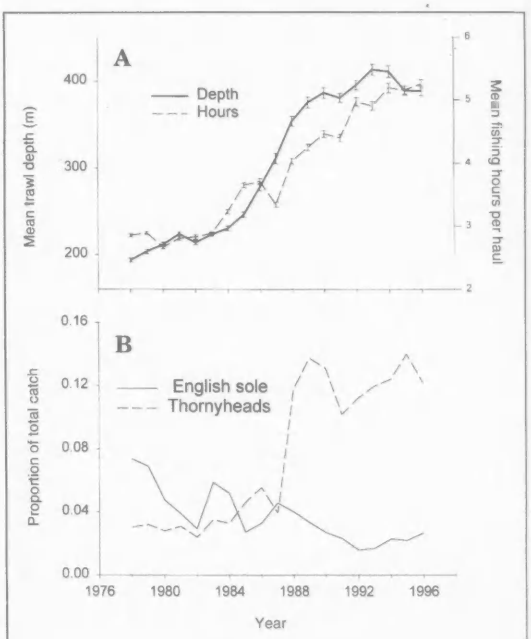

Figure 12

(**A**) Mean annual trawl depth and mean fishing hours per trawl haul off Eureka from 1978 to 1992. Error bars are standard error of the mean. (**B**) Proportion of total groundfish trawl catch of thornyheads and English sole from 1978 to 1994.

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Reproductive versus somatic tissue growth during the life cycle of the cuttlefish *Sepia pharaonis* Ehrenberg, 1831

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Abstract.—The effect of maturation on relative growth of somatic tissues was investigated by measuring and comparing monthly changes in dry weight of somatic tissues and reproductive organs. In both sexes, reproductive tissues grew in relation to total body mass; at maturity female reproductive tissue was 16% of total dry body mass, whereas male reproductive tissue was 2.6%. In females, the relative mass of the mantle and head decreased during maturation, whereas the relative mass of the viscera increased. In males, the mass of the viscera increased with maturation, but no decreases occurred. The percentage composition of protein in the mantle and head of females for each maturity stage did not differ significantly. For both sexes, the digestive gland mass remained relatively constant throughout the different maturity stages and seasons, and analysis of stomach fullness indicated that feeding increased in the final maturity stages. All observations support the hypothesis that energy and nutrients for maturation are supplied mainly by diet rather than by stored resources, but that during maturation there is a shift of emphasis from somatic growth to gonadal development and vitellogenesis. *Sepia pharaonis*, which appears to be an intermittent multiple spawner, does not use protein from muscle tissue for developing and growing its reproduction tissues.

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Cephalopod mollusks have various life history strategies, ranging from typically semelparous (e.g. many coleoids) to iteroparous (e.g. *Nautilus* spp.) (Boyle, 1983, 1987). Different modes of semelparity may occur, and this diversity may be related in part to growth patterns (Mangold et al., 1993). Most cephalopods that have been studied are fast growing, and they generally reproduce once and die (Calow, 1987). However, others have intermittent growth (Boletzky, 1987; Forsythe and Van Heukelem, 1987; Jackson and Choat, 1992) and multiple spawning events (Harman et al., 1989; Lewis and Choat, 1993). We investigated the relation between reproduction and somatic growth in the commercially valuable cuttlefish *Sepia pharaonis* Ehrenberg, 1831.

For many marine invertebrates, reproduction represents an enormous energy investment, and achieving the optimum balance between somatic and reproductive effort is critical to an individual's lifetime fitness (Calow, 1981). The variations in reproductive strategies usually correlate with variations in feeding and growth patterns. Assessing the cost of reproduction is difficult, and although slowing of somatic growth may indicate the allocation of energy to oocyte production, an assessment of somatic tissue may provide a better indicator of the cost of reproduction (Calow, 1983).

For example, in some benthic octopuses, mantle protein is mobilized to provide energy for egg development; the subsequent depletion of protein from body tissues probably contributes to the death of some octopus females (Tait, 1986; Pollero and Iribarne, 1988). This would not seem to be a sensible strategy for a swimming cephalopod, such as cuttlefish, which still requires functional muscle to survive in the water column. *Sepia pharaonis*, which migrates to spawning grounds from its feeding grounds (Gabr et al., 1998), would certainly need to maintain swimming ability.

Elucidation of patterns of energy storage and utilization is important in understanding the interaction between organism and environment (Clarke et al., 1994). Although many studies indicate that oocyte produc-

tion affects the growth and condition of somatic tissue in squid (e.g. Rowe and Mangold-Wirz, 1975; Hatfield et al., 1992), few studies have examined the expenditure of nutrients and energy for the development of reproductive organs in cuttlefish. Boucaud-Camou (1971) found that the digestive gland of *Sepia officinalis* has high concentrations of lipids, suggesting that it acts as a storage organ. Castro et al. (1991) studied changes in the digestive gland of *S. officinalis* and *S. elegans* throughout their life cycles and observed that the digestive gland weight of *S. officinalis* decreased progressively with starvation. However, there is no evidence that the digestive gland provides stored energy for gonad development.

Sepia pharaonis is widely distributed in the Indo-Pacific from the Red Sea to Japan and Australia. Together with *S. dollfusi*, it is the primary fishery in the Suez Canal and the most valuable commercial cephalopod in the northern Indian Ocean (Nesis, 1987). Little is known about the biology of this species (Silas et al., 1985; Aoyama and Nguyen, 1989; Gabr et al., 1998). In this paper, we examine aspects of its life history to determine if a trade-off exists between somatic and reproductive tissues. We measured food intake to determine whether nutritional activity was involved in the development of reproductive organs.

Materials and methods

Samples of *Sepia pharaonis* were collected monthly from Bitter Lake, the main fishing port in the Suez Canal, from September 1994 to April 1996. In total, 1428 females and 1151 males were examined. The dorsal mantle lengths ranged from 10 to 240 mm. Specimens were dissected to determine sex and maturity stage. Four maturity stages for each sex were determined by using a modification of the scale proposed by Mangold-Wirz (1963) and refined in detail for *Sepia pharaonis* by Gabr et al. (1998): for females, I=immature, II=maturing, III=pre-spawning, and IV=spawning; for males, I=immature, II=maturing, III=fully mature, and IV=spawning.

Dorsal mantle length (ML) and nidamental gland length (NGL) of females were measured to the nearest mm. The following measurements of mass were made to two decimal places (in grams): total body mass (BM); total somatic mass (SM); mantle mass (MM); head mass including arms and tentacles (HM); digestive gland mass (DGM); viscera mass (VM) including gills, stomach, caecum, pancreas, ink sac; ovary mass (OM) including oviduct; testis mass (TM); nidamental gland mass (NGM); and spermatophoric complex mass (SCM).

Relative assessment of somatic tissue growth

Two statistical analyses were conducted to determine if somatic tissue declined in relation to size during maturation. All statistical analyses were carried out by using the MINITAB statistical package and all data were $\log_{10}$-transformed.

In the first analysis, a multiple regression was applied to the female data only by using $\log_{10}$ mantle length and $\log_{10}$ nidamental gland length as independent variables. These variables were selected because they correlated with our maturity scale (Gabr et al., 1998). Multiple regression equations were obtained for log-transformed total somatic mass and for masses of mantle, head, digestive gland, viscera, and ovary (including oviduct and oviductal gland, and nidamental gland). This analysis allowed for the use of a continuous variable in the assessment of maturity over the whole size range of the sampled population. This multiple regression analysis was carried out only on females because length was used in the analysis. To carry out a similar exercise with male cuttlefish, the relation of the log-transformed mass of each organ with spermatophoric complex mass (SCM) and body mass would have to be used. These variables would lead to problems in scaling because they would involve autocorrelation, which would distort perceived relationships (LaBarbera, 1989). The ratio of SCM to ML has not been tested before as an objective measure of maturity in male cuttlefish and therefore no analysis was included here.

In the second analysis, a multivariate analysis of covariance (ANCOVA) was applied to the total somatic mass, individual somatic organs, and reproductive organs, whose relationships with the reproductive cycle were considered dependent variables (Garcia-Berthou and Moreno-Amich, 1993). Mantle length was treated as the covariate. A fundamental assumption of standard ANCOVA (McCullagh and Nelder, 1983) is the homogeneity of regression coefficients (slopes) of dependent variable and covariate relationships. This assumption can be tested with a special design of ANCOVA, by analyzing the pooled covariate by factor interaction. If the covariate by factor interaction is significant, standard ANCOVA should not be developed. Otherwise, if the covariant by factor interaction is not significant, the standard ANCOVA design is the preferred method. For the cases with significant effect with factor (maturity stage), the variation can be described by using the predicted means for each cell, adjusted for the effect of the covariate. We set the alpha level for statistical significance at 0.001 to identify the strongest effects of maturity on the dependent variables.

Dry weight analysis

To study the seasonal variation in somatic and reproductive organs, dry weight was used to correct for differences in water content between different organs. The samples for this study were collected from November 1994 to April 1996. From each monthly sample, a subsample of 20 females and 20 males was selected with mantle lengths within a 20-mm size range encompassing the mean size at maturity (the size at which 50% of the individuals were maturing or mature). This size was 122 and 61 mm ML (calculated by using the whole-year sample) for females and males, respectively (Gabr et al., 1998). It is possible to treat specimens from around the mean as "standard" animals (*sensu* Gabbott, 1976) and so compare cuttlefish at different degrees of maturity without having to make statistical corrections for size. There were no cuttlefish of maturity stage I in this subsample; however, stages II to IV were present. The cuttlefish in the subsample were dissected in the same way as those in the sample as a whole. The same measurements of mass to two decimal places (in grams) were taken, but dry rather than wet weight was used. Tissues were dried to constant weight (for 48 h) at 80°C and then cooled in a desiccator.

The following indices were calculated for dry weight tissues: gonadosomatic index for females (GSI) = 100 OM/BM; gonadosomatic index for males (GSI) = 100 TM/BM; nidamental gland index (NGI) = 100 NGM/BM; spermatophoric complex index (SCI) = 100 SCM/BM; mantle index (MI) = 100 MM/BM; head index (HI) = 100 HM/BM; digestive gland index (DGI) = 100 DGM / BM, and viscera index (VI) = 100 VM/BM.

Analysis of protein

The dry tissue of mantle and whole head for 7 to 9 females of maturity stages II–IV was ground to a fine powder with a mortar and pestle. The powdered samples were placed in sealed plastic vials and stored for further analysis. The Kjeldahl method for determination of nitrogen was used (see Giese, 1967). % Protein = % nitrogen × 6.25 (Giese, 1967; Rigby, 1990; Dickey-Collas, 1991). Kruskal-Wallis ANOVA was used to examine the significant variation in percentage of protein between maturity stages.

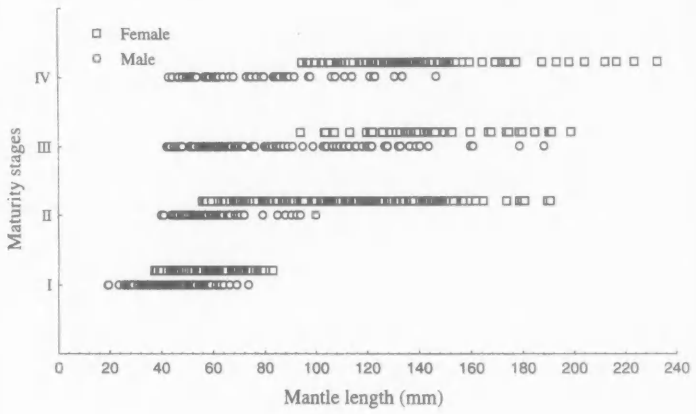

Figure 1
Relation between mantle length and maturity stages in female and male *Sepia pharaonis*.

Stomach content analysis

Each specimen's stomach fullness was estimated according to a 5-level subjective scale: 0=empty; 1=one-quarter full; 2=half full; 3=three-quarters full; 4=full or distended.

Length-weight relationship

Equations of the form $BW = aML^b$, where a and b are constants of the regression, were fitted by transforming the data into $\log_{10}$ and deriving the regression line by the least squares method. Correlation was expressed by the coefficient r^2, and comparisons between males and females were made by ANCOVA.

Results

Growth and maturity

Maturity generally increased with mantle length, but each stage was represented by a very wide range of mantle lengths with considerable overlap between stages (Fig. 1). This finding suggests that there is no strong relation between growth and maturation rate. Males attained full maturity (stage III) at a smaller size than females (stages III and IV).

Maturity stages versus soma production and gonad production

In females (Table 1), there was a significant increase in total somatic mass and mass of somatic organs

Table 1

Intercepts (a) and slopes (b_1 and b_2) ± SD for multiple regression equations relating mantle length (b_1) and nidamental gland length (b_2) to tissue masses for female *Sepia pharaonis*. The equation is log tissue mass = $a + b_1 \log ML + b_2 \log NGL$. P is level of significance (* indicates significant relationships i.e. $P<0.05$); s is residual standard deviation about the regression lines; r^2 is adjusted proportion of variation accounted by the variance model; and n is number of specimens.

	a	b_1	P	b_2	P	s	r^2	n
Independent variables:	mantle length; nidamental gland length							
Dependent variables:	0.0001*							
Total somatic mass	–0.87 ±0.05	2.92 ±0.04	0.0001*	–0.09 ±0.02	0.0001*	0.24	0.99	191
Mantle mass	–1.22 ±0.05	2.98 ±0.05	0.0001*	–0.14 ±0.02	0.0001*	0.59	0.98	226
Head mass	–1.21 ±0.04	2.84 ±0.04	0.0001*	–0.08 ±0.02	0.005*	0.25	0.99	191
Digestive gland mass	–2.20 ±0.10	2.98 ±0.11	0.0001*	–0.02 ±0.05	0.690	1.78	0.93	192
Viscera mass	–1.71 ±0.03	2.58 ±0.13	0.0001*	0.03 ±0.06	0.580	2.4	0.89	192
Ovary mass	0.49 ±0.36	–1.66 ±0.41	0.001*	3.50 ±0.16	0.0001*	17.33	0.93	176
Nidamental gland mass	–0.17 ±0.26	–0.65 ±0.29	0.030	2.92 ±0.11	0.0001*	9	0.96	176

(i.e. mantle, head digestive gland and viscera masses) with mantle length ($P<0.05$). The effect of ML on reproductive organ mass (i.e. ovary, nidamental gland masses) also was significant ($P<0.05$). In relation to nidamental gland length, there was a small but significant decrease ($P<0.05$) in total somatic mass, mantle mass, and head mass, whereas the relative decrease in digestive gland mass and viscera mass was not significant ($P>0.05$). As expected, there was also a highly significant increase ($P<0.05$) in reproductive organ mass with maturity (NGL).

The second analysis was an analysis of multivariate covariance (ANCOVA). In an animal that matures at a wide range of body sizes, it is difficult to quantify the pattern of maturation because comparisons of individuals of different sizes cannot be thought of as indicating the pattern of growth and maturation of any one animal. Thus, although some animals matured at 60 mm ML, others remained immature at larger sizes (Fig.1). ANCOVA corrects for the variation in size (ML) of animals within maturity stages.

Table 2 shows the initial standard ANCOVA design to test for homogeneity of slopes. In females, there was significant effect of an interaction between the factors (maturity stage) and covariate (mantle length) for OM and NGM. The effect of interaction of mantle length and maturity stages on TSM, MM, HM, DGM, and VM was not significant ($P>0.001$). Thus in these cases the hypothesis of homogeneity of slopes was accepted; therefore further analyses were required to test the effect of maturity stages for these variables. In males, there was a highly significant effect ($P<0.001$) between mantle length and maturity stage for all log-transformed dependent variables except spermatophoric complex mass. Thus for these variables the hypothesis of homogeneity of slopes was rejected and further analysis was not possible (i.e. the standard ANCOVA design should not be developed for these cases).

The results of the final ANCOVA design (in the cases where the effect of mantle length and maturity stage interactions were not significant) are indicated in Table 3. In female *Sepia pharaonis*, maturity significantly affected TSM, MM, HM, and VM ($P<0.001$) but did not significantly affect DGM ($P>0.001$). In males, maturity significantly influenced spermatophoric complex mass ($P<0.001$).

Figure 2 shows the adjusted means for each dependent variable for each maturity stage after the removal of the mantle length (covariate) effect when the effects of maturity stages were found to be significant. For females, there was a decrease in total somatic mass, mantle mass, and head mass with increasing maturity stage. There was a decrease in viscera mass from stage I to stage III followed by an increase at stage IV (Fig. 2A). For males, there was an increase in relative mass of spermatophoric complex mass with increasing maturity stage (Fig. 2B).

Monthly variation in soma versus gonad production

Monthly fluctuations in mean dry weight indices for individual organs of somatic tissue (mantle index, MI; head index, HI; digestive index, DGI; and viscera index,VI) and reproductive tissue (gonadosomatic index, GSI; nidamental gland index, NGI; and spermatophoric complex index, SCI) for females and males are illustrated in Figures 3 and 4, respectively. These indices displayed monthly fluctuations and indicated the relative proportion that each body component contributed to the weight of the entire body. The mantle mass was always the largest component

Table 2

Preliminary design of ANCOVA for *Sepia pharaonis*. In each case, mantle length is the covariate, maturity stage (I–IV) is the factor, and the dependent variables are total somatic mass (TSM), mantle mass (MM), head mass (HM), digestive gland mass (DGM), viscera mass (VM), ovary mass (OM), nidamental gland mass (NGM), testis mass (TM), and spermatophoric complex mass (SCM). The homogeneity of slopes was tested with a pooled covariate by factor interaction: *F*-statistic. Significance levels ($P<0.001$) are indicated by an asterisk.

	Mantle length (ML)		Maturity stages (MSt)		ML × MSt	
	F	*P*	*F*	*P*	*F*	*P*
Female						
TSM	11000.00	<0.001*	2.80	0.039	1.87	0.130
MM	11000.00	<0.001*	4.74	0.003	2.81	0.030
HM	10000.00	<0.001*	5.29	0.001	3.93	0.009
DGM	3440.00	<0.001*	2.18	0.089	2.16	0.092
VM	2926.30	<0.001*	0.40	0.754	0.98	0.400
OM	271.07	<0.001*	25.15	<0.001*	29.87	<0.001*
NGM	513.73	<0.001*	166.10	<0.001*	317.58	<0.001*
Male						
TSM	918.60	<0.001*	22.00	<0.001*	23.00	<0.001*
MM	1745.94	<0.001*	14.32	<0.001*	13.66	<0.001*
HM	1295.97	<0.001*	12.50	<0.001*	11.02	<0.001*
DGM	849.18	<0.001*	11.15	<0.001*	9.55	<0.001*
VM	853.13	<0.001*	5.96	<0.001*	5.28	<0.001*
TM	612.65	<0.001*	294.18	<0.001*	15.52	<0.001*
SCM	749.19	<0.001*	6.01	<0.001*	0.88	0.450

proportionally, followed by the head mass. Thus, *S. pharaonis* weight gain and loss were accounted for mainly by the mantle and head mass that underwent fluctuation in mean dry weight index during the study.

The MI and HI diminished considerably as gonad development proceeded. The largest decrease in MI and HI of females occurred in spring and summer (from March to September), as shown in Figure 3. These indices decreased from 52% to 41% and from 34% to 28%, respectively. In contrast, during the same period the gonads (GSI, NGI) exhibited development; GSI increased from 1% to 9% and NGI increased from 2% to 7%. VI increased rapidly from May to November, from 5% to 10%. DGI showed little change over the whole sampling period (ranging between 7% and 10%).

By contrast, in male *Sepia pharaonis*, the MI, HI, and DGI remained relatively constant throughout the entire sampling period (Fig. 4). The pattern of VI was consistent with the situation in female, increasing from 5% to 8% during the period from May to October. There was a gradual increase in GSI and SCI from November, reaching the highest value in May (≈1.3%), and spawning after June was indicated by a decline in GSI and SCI.

Table 3

Final design of ANCOVA for *Sepia pharaonis* data for which the homogeneity hypothesis was accepted, *F*-statistics, and *P*-values. See Table 2 for definitions of abbreviations. Significance levels ($P<0.001$) are indicated by an asterisk.

	Mantle length (ML)		Maturity stages (MSt)	
	F	*P*	*F*	*P*
Female				
TSM	15000.00	<0.001*	25.130	<0.001*
MM	16000.00	<0.001*	40.570	<0.001*
HM	14000.00	<0.001*	10.470	<0.001*
DGM	4770.00	<0.001*	0.680	0.560
VM	4031.89	<0.001*	11.270	<0.001*
Male				
SCM	901.800	<0.001*	133.890	<0.001*

Percentage of protein, water content, and maturity stage

The mean percentage composition of protein and mean percentage of water content in the mantle and head of females for maturity stages II–IV is shown

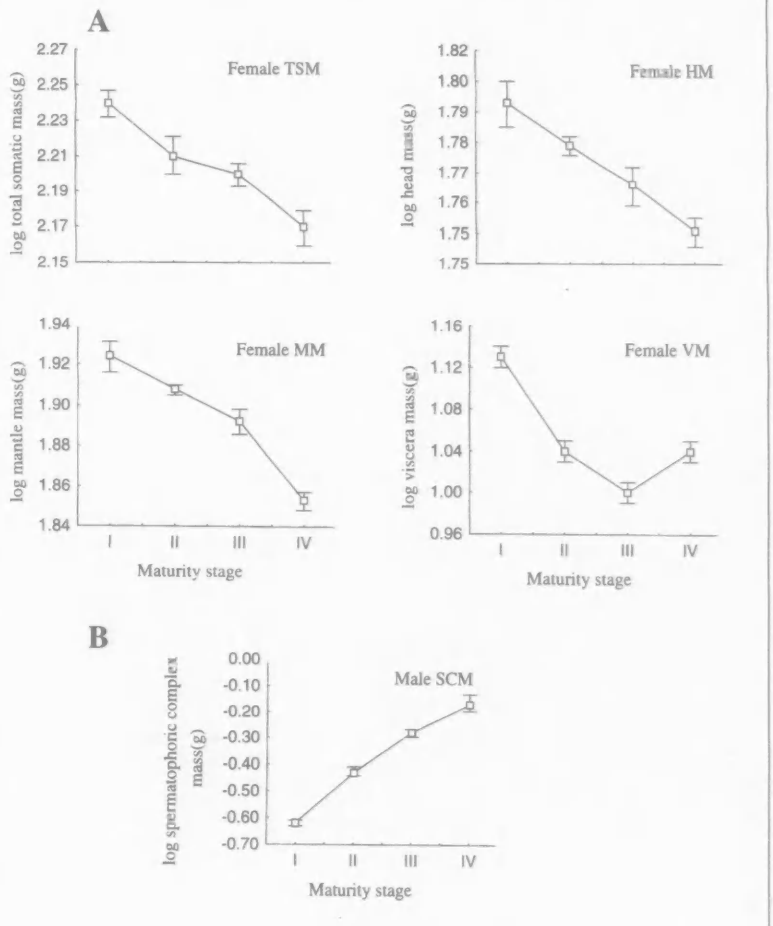

Figure 2

(**A**) Adjusted means (SD) for dependent variables (total somatic mass, TSM; mantle mass, MM; head mass, HM; viscera mass,VM) at each maturity stage for female *Sepia pharaonis*. (**B**) Adjusted means (SD) for dependent variable spermatophoric complex mass (SCM) for males. Adjusted means (SD) were obtained by analysis of covariance removing the effects of the covariate (mantle length).

in Table 4. In neither mantle nor head was there significant variation ($P>0.05$) in percentage of protein or water content with maturity stage.

Stomach fullness in relation to maturity stages

The stomach fullness for each maturity stage for each sex is illustrated in Figure 5. The degree of stomach fullness remained relatively constant through the maturity stages, indicating that *Sepia pharaonis* continued to feed when mature.

Length-weight relationship

The length-weight relationship for *Sepia pharaonis* is described by the equation: $Wt = 0.27L^{2.65}$, $r^2 = 0.99$, $n = 966$ for females, and $Wt = 0.28L^{2.60}$, $r^2 = 0.99$, $n = 723$ for males. The elevation and slopes from the regression equations for females and males did not differ significantly, thus indicating that females have approximately the same weight as males at the same mantle length, and that both sexes increase similarly in weight per unit gain in mantle length.

Discussion

This study describes the pattern of allocation of resources to the growth of somatic and reproductive tissues in *Sepia pharaonis*, one of the two most commercially important cephalopods in the Suez Canal and northern Indian Ocean. This study indicates that gametogenesis is fueled by energy and nutrients derived from the diet rather than from reallocation of somatic reserves. Two complementary methods (analysis of covariance and multivariate regression on the entire data set) and the monthly changes in dry weight of somatic indices of a restricted size range showed essentially similar patterns of maturation.

Sexual maturation in *Sepia pharaonis* affected males and females differently. Forsythe and Van Heukelem (1987) suggested that male maturity in cephalopods was achieved at little cost to somatic growth and that, in most cases, males continue to grow after reaching maturity. Changes in male somatic mass do not appear to be related to maturity. At full maturity in males, dry weight of reproductive and accessory reproductive tissues accounted for only 2.6% of the total somatic dry weight. However, these tissues accounted for approximately 16% in females. For both sexes, somatic growth was completed by late October as the average mantle mass and head mass components reached maximum weights.

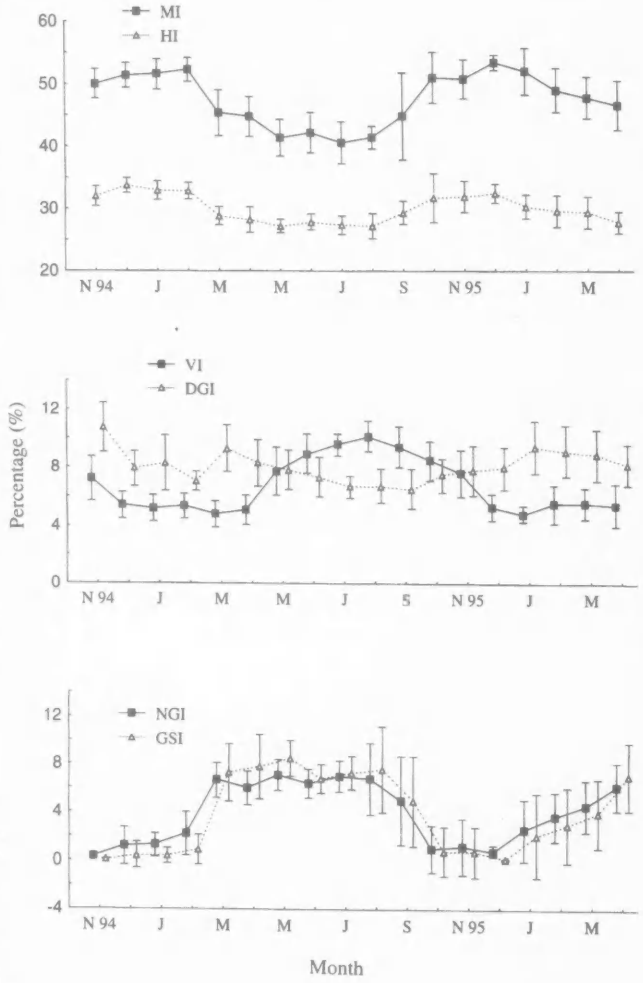

Figure 3

Female *Sepia pharaonis* mean (SD) dry weight indices of mantle (MI), head (HI), viscera (VI), digestive gland (DGI), nidamental gland (NGI), and gonad masses (GSI) for standard size (110–130 mm ML).

In females, spawning occurred from spring throughout the summer, and the end of spawning activity was reflected by a sharp drop in the average gonad weight index in October (Fig. 3) . Thus spawning occurred at the time of increasing temperature and food availability (Gabr, unpubl. data). There was no evidence of decline in feeding rate with maturation. This finding suggests that gonadal growth may be supported directly by the assimilated food ration, although some diversion of resources into reproduction at the expense of somatic growth also occurred. This diversion of resources was indicated by a small but significant decrease in mantle and head mass with maturation (Fig. 2), and the inverse relationship of mantle and head mass with gonadal indices (Fig. 3).

There is some evidence to support the idea that female *Sepia pharaonis* may feed, grow, and mature simultaneously in the field. For example, no spent females were caught at any time of the year. This may be because it is difficult to differentiate spent females from mature ones if spent females remain in good condition (because they continue to feed when mature). Because females need a greater energetic reserve for reproduction, they grow faster than males and reach a maximum size of 240 mm ML, whereas the maximum size for males was 170 mm ML. *Sepia pharaonis* spawns in shallow water and migrates

offshore after spawning either to die or to return to spawn again; such a migration is unlikely to be preceded by any degradation of mantle muscle, which is the major organ for locomotion in cuttlefish. In neither mantle nor head was there a significant variation in percentage of protein or water content with maturity stage. These data indicate that female *S. pharaonis* possibly do not use mantle or head tissue to fuel gonadal development, at least during the beginning of the spawning season.

In sharp contrast, studies of another cuttlefish, *Sepia dollfusi* (Gabr et al., in press), have demonstrated that this species seems to use mantle muscle as an energy source during gonadal development. There thus appears to be a continuum in cuttlefish reproductive strategy. At one end, spawning is associated with gonad maturation at the expense of somatic tissue. At the other end, growth of reproductive organs takes place through the use of energy and nutrients derived from the diet, not through mobilization of nutrients and energy from somatic tissue.

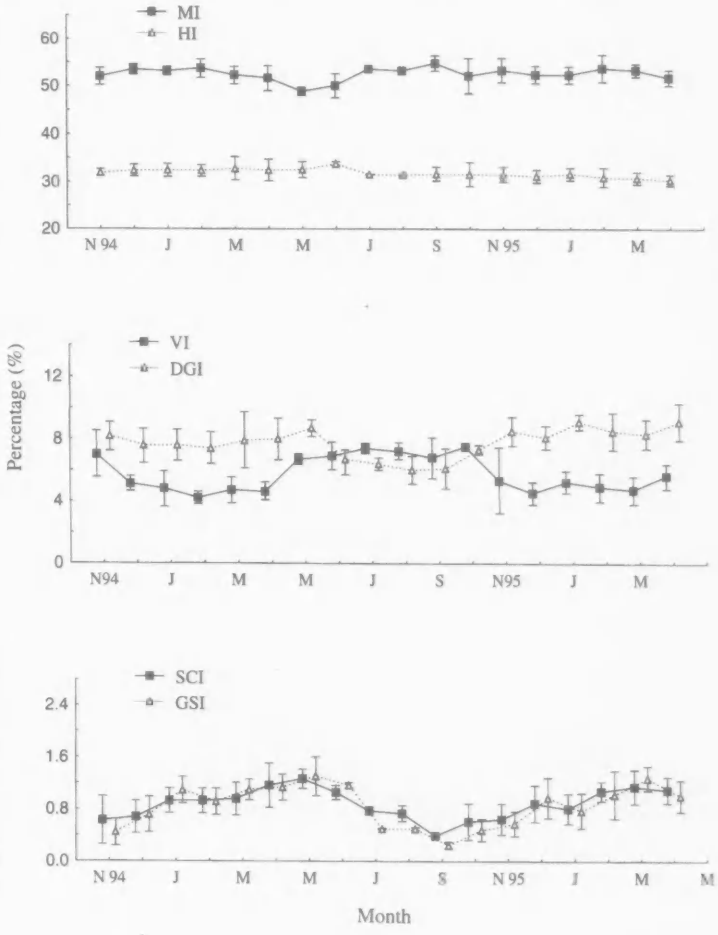

Figure 4

Male *Sepia pharaonis* mean (SD) dry weight indices of mantle (MI), head (HI), viscera (VI), digestive gland (DGI), spermatophoric complex (SCI) and gonad masses (GSI) for standard size (50–70 mm ML).

The results of this paper agree with some studies on the squid *Illex argentinus* (Hatfield et al., 1992; Rodhouse and Hatfield, 1992; Clarke et al., 1994). Although mantle mass of female *Illex argentinus* decreases in relation to ML with maturity, this is not associated with degradation or changes in the biochemical composition of mantle muscle. Studies on *Loligo forbesi* (Collins et al., 1995), *L. gahi* (Guerra and Castro, 1994) and *Photololigo* sp. (Moltschaniwskyj, 1995) have also demonstrated that maturation and growth occur simultaneously during most of the life cycle and that the condition of the squid remains high at maturation.

The digestive gland showed no loss of mass during maturation. Boucaud-Camou (1971) indicated that the digestive gland of *Sepia officinalis* could act as a lipid storage organ, and Blanchier and Boucaud-Camou (1984) found that the variation in lipid levels of the digestive gland seemed more related to diet than to sex or maturity state of the gonads. There was no significant variation in the digestive gland weight with maturity state and season. Thus, the digestive gland mass cannot be used as an indicator of feeding activity in *S. pharaonis* as it can in some squid (Abolmasova et al., 1990) because no increase in DGI was found in the season of high feeding activity. This agrees with Castro et al. (1991), who found no significant variation in the digestive gland weight with season in *S. officinalis* and *S. elegans*.

In conclusion, this study shows that the pattern of intermittent spawning suggested by our previous

Table 4

Summary of mean ± SD values of percentage of protein and water content in mantle and head dry tissue with maturity stages for female *Sepia pharaonis*.

		% Protein			% Water content	
Maturity stage	Number	Mantle	Head	Number	Mantle	Head
II	9	78.33 ±0.68	76.21 ±0.32	66	75.83 ±1.4	79.38 ±1.4
III	8	79.78 ±0.41	76.23 ±0.39	20	76.18 ±1.3	79.64 ±1.06
IV	7	78.19 ±0.39	75.82 ±0.53	79	75.48 ±1.8	78.91 ±1.5
Kruskal-Wallis ANOVA:	*H*	2.08	0.24		1.32	3.37
	P	0.35	0.88		0.51	0.18

study of this species (Gabr, et al., 1998) is quite likely, partly because the spawning season is greatly protracted (Fig. 3). Indeed, it appears that this species is capable of meeting the demands of oocyte production without metabolizing reserves of other tissues. Both males and females continue to feed as maturity is reached, thus energy for gonad production is diverted primarily from the food supply, although some diversion from somatic tissue may also occur. In the context of this paper and results from *S. dollfusi* (Gabr et al., in press), variation in reproductive strategies correlates with variations in feeding and growth patterns as suggested previously for other coleoids (Mangold et al., 1993).

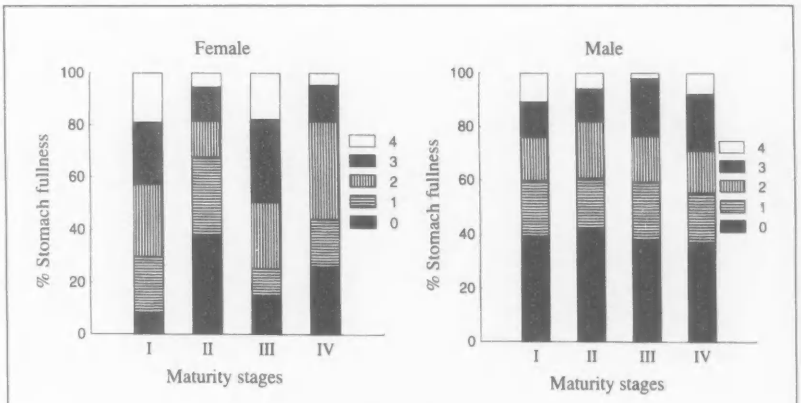

Figure 5

Stomach fullness for each maturity stage of both sexes of *Sepia pharaonis*. 0 = empty; 1 = one-quarter full; 2 = half full; 3 = three-quarters full; 4 = full or distended).

Acknowledgments

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Aging methods for yellowtail kingfish, *Seriola lalandi*, and results from age- and size-based growth models

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Abstract.—Dorsal spines, otoliths, scales, and vertebrae collected from yellowtail kingfish (*Seriola lalandi*) in NSW, Australia, were assessed for usefulness in estimating age. Legibility of growth zones, the time scale at which zones form, and precision of age estimates were evaluated for fish sizes from 323 to 1090 mm FL. All calcified structures contained growth zones, but dorsal spines were unsuitable for age determination because it was likely that early growth zones were lost. From marginal increment analysis, it appeared that one zone was laid down per year for otoliths and possibly scales, but a clear pattern was not found for vertebrae. Although exact agreement between repeated age readings was relatively low (50–66%), agreement within one zone was higher (92–96%) and scales provided the most precise readings. Precision decreased with increasing age of fish. Growth curves derived from otoliths and scales were similar for all ages except fish from the first age class; those derived from otoliths and vertebrae were similar for all fish with less than eight growth zones. Although statistical differences were found between the growth curves of scales and vertebrae for some age classes, with the exception of the first age class these differences were not biologically important. Growth rates estimated from length-frequency (age-based) and mark-recapture (length-based) data compared favorably with those estimated from calcified aging structures. Otoliths, scales, and vertebrae all showed promise as structures for aging kingfish, but further work is needed to determine the position of the first zone and to validate estimates for all age classes. Until such work is completed, we recommend that scales and either otoliths or vertebrae be used for aging kingfish.

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Yellowtail kingfish, *Seriola lalandi*, is a popular recreational species and supports significant commercial fisheries throughout temperate regions of the world. In Australia, the major commercial fishery for yellowtail kingfish is in New South Wales where 400–600 tonnes are caught per year. Despite the existence of a commercial fishery and persistent controversy about exploitation of the species, very little is known about its biology. For future management of the fishery and for stock assessment purposes, information on age and growth is needed.

Estimates of age of *Seriola* spp. have been derived from a variety of methods and structures, reflecting the difficulty of aging *Seriola* and other pelagic species. The Japanese species (*Seriola quinqueradiata*) is the most studied species in the genus because of its importance in aquaculture. Studies in the 1950s used scales, vertebrae, and opercular bones for aging (e.g. Mitani, 1955, 1958; Mitani and Sato, 1959). More recent studies have focused on the use of vertebrae (e.g. Munekiyo et al., 1982; Murayama, 1992). Scales have also been used to age *S. lalandi* (formerly *S. dorsalis*, Baxter, 1960), as have otoliths (Penney[1]). Recently, sectioned otoliths were used to determine ages of *Seriola dumerili*, although it was acknowledged that age and growth determinations were difficult (Manooch and Potts, 1997). Despite the use of a variety of structures for aging *Seriola* spp., there has been no comparative analysis to determine which structure provides the most reliable estimates. In addition, most studies have assumed that growth zones are annual and there have been few validations of age estimates (but see Mitani and Sato, 1959; Baxter, 1960).

The specific objectives of this study were 1) to assess the usefulness of several structures (scales, otoliths, dorsal spines, and vertebrae) for determining the age of kingfish, 2) to compare multiple age estimates for different structures in order to determine the most precise method for determining age and growth parameters, 3) to provide information on size-at-age and 4) to compare growth rates obtained

[1] Penney, A. J. 1992. Sea Fisheries Research Institute, Private Bag X2, Rogge Bay 8012, South Africa. Personal commun.

from age-length data (from counts of zones in calcified structures) to those obtained from length-frequency and mark-recapture (tagging) data. We acknowledge that the data from these three approaches for estimating growth are not directly comparable (Francis, 1988a), but follow the recommendations of Francis (1995) in interpreting differences.

Materials and methods

Fish collection and treatment

Yellowtail kingfish, *Seriola lalandi*, specimens were collected from New South Wales, Australia, between August 1995 and July 1996 by commercial or recreational fishermen. Fish caught by commercial fishermen were obtained after being processed by filleting. Fish were measured (total length, fork length) and sagittal otoliths, dorsal spines, scales, and vertebrae removed. Dorsal spines were examined but considered unsuitable for aging because the center (core) region was either occupied by vascular bony tissue or was hollow. The hollow core in large fish was found to have a larger diameter than the whole spine of small fish. For this reason, it was likely that early growth zones were lost in older fish and therefore spines were considered unsuitable for aging.

Sagittae

Whole sagittae were burned for 7 min at 500°C. They were viewed under a low-power dissecting microscope (6× magnification) with reflected light against a black background. Assignments of age were based on counts of opaque (light) zones or ridges (or both) that were usually most visible at the base of the rostrum on the ventral surface (Fig. 1A). Sagittae were also embedded in clear resin, sectioned in a transverse plane with a low speed saw, the sections (≈350 mm thickness) mounted on glass slides, and viewed under a compound microscope (40× magnification) with reflected light against a black background.

Scales

Scales were removed from a position anterior and ventral to the pectoral fin. It was necessary to remove scales from such a position because most fish had been processed prior to the removal of scales. Scales from each fish were soaked in a solution of sodium hydroxide for 3 h, then rinsed and soaked in water for a further 3–12 h. Clean, nonreplacement (i.e. original scales showing typical ctenoid shape) scales were dry-mounted between two glass microscope slides. Scales were read under a compound microscope (20× magnification) with reflected light against a black background. Presumed annuli were identified by cutting over (*sensu* Bagenal and Tesch, 1978) in the lateral fields or by clear zones, where circuli were more widely spaced, in the anterior field.

Vertebrae

The second vertebra of 24 vertebrae present in kingfish was chosen because it was most easily obtained from processed fish. Vertebrae were either stored frozen with flesh intact, or the flesh was removed, and the vertebrae were separated from each other and stored dry. The spines were removed and each vertebra cut in half along the longitudinal–horizontal plane and stained in a solution of alizarin red S (following Berry et al., 1977) for 8 h, rinsed in tap water for at least 1 min, and dried at room temperature. Vertebrae were read under a dissecting microscope (6–12× magnification) with reflected light from a blue-filtered, high-intensity bulb against a black background. Age was estimated from counts of ridges on the inner surface of the vertebra from the core to the outer edge of the centrum (Fig. 1C).

Assessment of aging techniques

To determine whether the zones would be reliably interpreted, two replicate counts of zones were made for each structure by the same person. Counts were usually separated by one month. All readings were done in a random order, with no knowledge of date of collection, size of fish, or knowledge of previous counts. Preliminary investigations of transverse sections of otoliths from 50 fish (ranging from 323 to 1090 mm FL) found that growth zones were not interpretable for any fish (Fig. 2).

Multiple counts of zones (two counts for each aging structure) were used to estimate the probability of assigning an age a to a fish with estimated "true" age b following maximum-likelihood estimation procedures outlined in Richards et al. (1992). This procedure requires the estimation of a classification matrix where there are columns for each "true" age and rows for each assigned age, and the entries refer to probabilities of assigning age a to a fish, given its true age b. "True" age is best described as the most probable age, and it does not refer to the accuracy of the age estimate nor does it substitute for age validation procedures. It is assumed that fish will be assigned to the true (or most probable) age class with the highest probability (Richards et al., 1992).

The classification matrix is defined by up to four parameters, where the first two parameters, σ_1 and

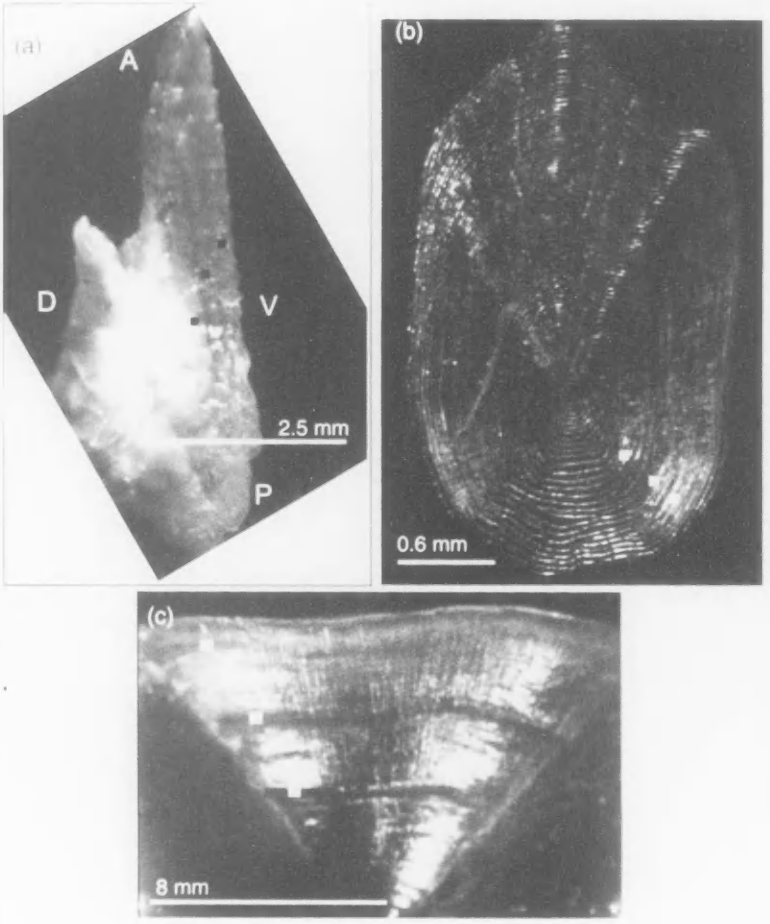

Figure 1

Structures used to estimate the age of kingfish from New South Wales: (**A**) otolith (860 mm FL, age 3); (**B**) scale (618 mm FL, age 3); and (**C**) vertebra (720 mm FL, age 3). All structures viewed with reflected light against a black background. Size of scale bars are indicated on each figure. Growth zones are indicated by squares; abbreviations: A = anterior, P = posterior, D = dorsal, V = ventral.

σ_A, are estimates of the standard deviation for the observation a at age 1 and A respectively. The third parameter, α, determines nonlinearity of $\sigma(b)$, the standard deviation of the observation a. The fourth parameter, β, controls the extent that the classification matrix may be dominated by its diagonal entries (Richards et al., 1992). Two possible representations of the classification matrix were used, namely a normal and an exponential representation (*sensu* Richards et al., 1992, p. 1803) and the α parameter was constrained to 0 during one fit of each of the normal and exponential representations, allowing four different cases of the model to be fitted for each aging structure. The appropriate model structure, or best fit model, for the classification matrix was then selected by using the Akaike information criterion (AIC) where a model with a low AIC value in relation to other models was considered to provide a good fit (Richards et al., 1992).

Initially, data from each aging structure (otoliths, scales, and vertebrae) were analyzed separately and an age assigned to each fish from each structure. The

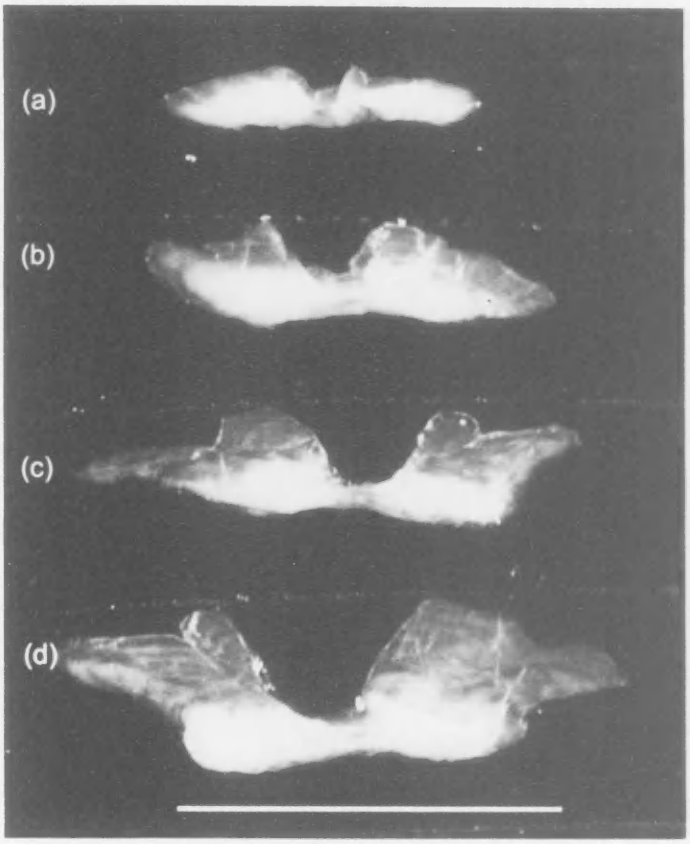

Figure 2

Transverse sections of sagittal otoliths of kingfish over a range of sizes viewed with reflected light against a black background: (**A**) 337 mm FL; (**B**) 638 mm FL; (**C**) 850 mm FL; and (**D**) 1002 mm FL fish. Scale bar is 1.5 mm.

classification matrix for the best model (see above) was used to estimate the most probable age of each fish by determining the probability that a fish would be from each true age class given its two assigned ages. Each fish was assigned to the age class with the highest probability (Richards et al., 1992). This estimate of age was used for growth models. Only the first five age classes (0–4) were used in the classification matrix because, although older fish occurred, sample sizes were small and some extrapolation for missing age classes would be necessary. Because data from older fish are important in estimating growth models, fish not used in the classification matrix were assigned an age by randomly selecting one of their two age readings.

The data matrix comprising the two age readings for each of the three aging structures was then examined to determine possible effects of the different aging structures and to determine a final age for each fish. Classification matrices for each aging structure were determined following a modification of the methods of Richards et al. (1992; outlined above). Results from running the models for each structure separately showed that the model of best fit was obtained by using a normal model with $\alpha = 0$; therefore, in its simplest form, the model contained the parameters σ_1, σ_A, and terms for the relative bias of each method (r_1 and r_2; $r_3 = 0 - r_1 - r_2$). Parameters determining the change in bias with age (γ) and nonlinearity of bias with age (η) were also added alone and indexed by aging structure. Different combinations of the model parameters were therefore tested to determine which model provided the best fit to the data and to determine relative biases by method.

Table 1

Summary of the different cases of Schnute's (1981) size-at-age growth model that was fitted to age estimates from different calcified structures and Francis's (1995) mark-recapture analogue of Schnute's growth model that was fitted to the tagging data.

	Schnute's (1981) size at age model	Francis's (1995) mark-recapture analogue of Schnute's (1981) growth model
Case 1: a≠0, b≠0	$Y(t)=\left[y_1^b+(y_2^b-y_1^b)\frac{1-e^{-a(t-\tau_1)}}{1-e^{-a(\tau_2-\tau_1)}}\right]^{\frac{1}{b}}$	$\Delta Y=-Y_t+\left[Y_t^b e^{-aM}+c(1-e^{-aM})\right]^{\frac{1}{b}}$
Case 2: a≠0, b≠0	$Y(t)=y_1\exp\left[\log(y_2/y_1)\frac{1-e^{-a(t-\tau_1)}}{1-e^{-a(\tau_2-\tau_1)}}\right]$	$\Delta Y=-Y_t+Y_t^{\exp(-aM)}\exp\left[c(1-e^{-aM})\right]$
Case 3: a≠0, b≠0	$Y(t)=\left[y_1^b+(y_2^b-y_1^b)\frac{t-\tau_1}{\tau_2-\tau_1}\right]^{\frac{1}{b}}$	$\Delta Y=-Y_t+\left[Y_t^b+(\lambda_1^b-y_1^b)\Delta t\right]^{\frac{1}{b}}$
Case 4: a≠0, b≠0	$Y(t)=y_1\exp\left[\log(y_2/y_1)\frac{t-\tau_1}{\tau_2-\tau_1}\right]$	$\Delta Y=-Y_t+Y_t(\lambda_1/y_1)^M$
Meaning of terms	$Y(t)$ = fish size (FL) at age t, τ_1 and τ_2 = lower and upper ages of fish respectively where $\tau_2>\tau_1$, y_1 and y_2 = mean sizes at ages τ_1 and τ_2, respectively. a and b describe the shape of the curve.	ΔY = mean growth Y_t = size at marking y_1 and y_2 = lower and upper sizes of fish, respectively, where $y_1<y_2$ g_1 and g_2 = mean annual growth for fishes of sizes y_1 and y_2 respectively, b = describes curvature in model, $\lambda_1=y_1+g_1$ and $\lambda_2=y_2+g_2$, $a=\ln\left[\frac{y_2^b-y_1^b}{\lambda_2^b-\lambda_1^b}\right]$ if $b\neq 0$ or $a=\ln\left[\frac{\ln(y_2/y_1)}{\ln(\lambda_2/\lambda_1)}\right]$ if $b=0$, $c=\frac{y_2^b\lambda_1^b-y_1^b\lambda_2^b}{\lambda_1^b-y_1^b+y_2^b-\lambda_2^b}$ if $b\neq 0$ or $c=\frac{\ln(y)\ln(\lambda_1)-\ln(y_1)\ln(\lambda_2)}{\ln(\lambda_1 y_2)-\ln(\lambda_2/y_1)}$ if $b=0,\Delta t=1$

To determine the timing of zone formation, the edges of the various structures were examined. The growth of the structure, subsequent to the most recent zone, was estimated as a percentage (20, 40, 60, and 80%) of the previously completed zone. It was also noted whether the zone was considered to be on the edge of the structure. Only fish with 2–4 growth zones were used. Fish were examined individually by structure in a random order with no knowledge of date of collection.

Estimation of growth models from calcified structures

Growth models using age estimates from different calcified structures were derived by using procedures outlined in Schnute (1981). Schnute's model relates size (FL) to age by several parameters, including two that describe the shape of the curve (a and b; Table 1). These latter parameters combine to describe a range of common growth curves, including the von Bertalanffy ($a>0$, $b=1$), Richards ($a>0$, $b<0$), logistic ($a>0$, $b=-1$) and Gompertz ($a>0$, $b=0$) (Table 1; Schnute, 1981). The other parameters in Schnute's growth model were y_1 and y_2, the mean sizes at ages τ_1 and τ_2 respectively, where the value of τ_1 and τ_2 are specified, but usually chosen to be near the lower and upper ends of the range of ages in the data. In this study, τ_1 and τ_2 were set at 1 and 5 respectively. All growth models were calculated by minimizing sums of squares and using additive errors because variation in size-at-age was similar for all ages of fish (see "Results" section).

Initially, a two-parameter model (y_1 and y_2) was fitted to the data (case 4 in Table 1). Two types of a three-parameter model [parameters were a, y_1, and y_2 (case 2), and b, y_1, and y_2 (case 3)] and a four-

parameter model (a, b, y_1, and y_2, case 1) were then fitted to the data (Table 1). To determine whether the addition of extra parameters resulted in a significantly better fit, significance tests based on the F-distribution were used (Schnute, 1981). Where the same number of parameters were present in the models (e.g. comparison of the two models with three parameters), the model with the lowest residual sums of squares was selected as the best fit.

Estimation of rates of growth from tagging data

Seriola lalandi tagged as part of the NSW Fisheries Gamefish Tagging program (Pepperell, 1985, 1990) were used to estimate growth. A major limitation of these data were that measurement methods were not standard and some measurements appeared spurious. Although most anglers measured total length, some measured fork length only. Where this occurred (17% of fish), fork length (mm) was converted to total length with the equation TL (mm)=1.122 × FL + 9. This equation was calculated from fish obtained for aging in which both fork and total lengths were measured (n=570). All fish for which tagging data were available (n=816) were initially included in analyses even if the data were highly improbable, as with measurements indicating shrinkage between 100 and 350 mm (Fig. 3A).

Growth estimates were obtained from the tagging data by using the maximum-likelihood method and the computer program GROTAG (Francis, 1988b). The growth model fitted was Francis's (1995) mark-recapture analog of Schnute's (1981) size-at-age model (Table 1). This model provides estimates of g_1 and g_2, the mean annual growth of fish of lengths y_1 and y_2 respectively, where y_1 and y_2 are chosen to span the range of lengths at tagging. A simple three-parameter model was initially fitted and then additional parameters (growth variability, seasonal growth variation, measurement error, and curvature in the model) were added in a stepwise manner by selecting the parameter that gave the greatest increase in log likelihood. At each step, likelihood ratio tests were used to determine whether addition of parameters resulted in significantly better fits (Francis, 1988b). Better estimates of the growth parameters can be obtained if measurement error is known (Francis, 1995). There was no way of estimating measurement error without using the current data set; therefore, measurement error was not fixed and this may have compromised estimates of growth. After fitting of the growth model, plots of residuals against length at tagging, time at liberty and expected growth increment were examined for any possible lack of fit of the model.

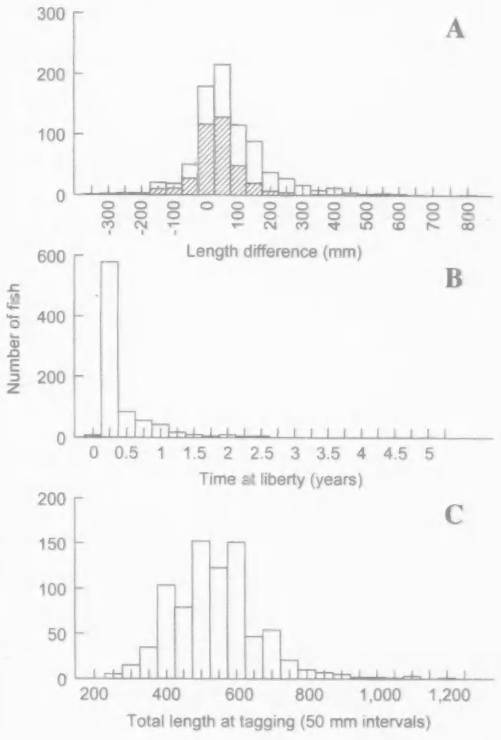

Figure 3

Distribution of (**A**) differences in length between tagging and recapture, (**B**) time at liberty and (**C**) length-at-tagging for kingfish (n=816). Fish recaptured within 30 days are also indicated in A with shading (n=384). Time at liberty (B) includes a small number of fish recaptured the same day that they were tagged (time at liberty=0).

Estimation of rates of growth from length-frequency data

Length-frequency data were obtained from fish sold at the Sydney Fish Markets between November 1985 and December 1989, prior to the introduction of a size limit of 600 mm TL in February 1990. Data were collected haphazardly amongst months and at locations ranging from 30°S to 37°S. Fork length of fish was measured to the nearest 10 mm and the sampling date and fishing area were recorded. Measurements of approximately 16,000 fish were made, enabling stratification of samples by month but not by year or area.

The von Bertalanffy (VB) model was fitted to the time series of 12 monthly length-frequency distributions by using MULTIFAN software (Fournier et al., 1990, 1991). Likelihood-based methods were used to simultaneously analyze the length-frequency distri-

butions sampled at different times to estimate the number of cohorts in the population, the growth parameters (asymptotic length [L_∞] and growth coefficient [K] of the von Bertalanffy growth equation), the age of the first cohort (assuming that the VB curve passes through the origin) and the proportions at age. The simplest model assumes that mean lengths-at-age lie on the VB growth curve and that the standard deviations of length-at-age are identical for all cohorts. More complex models were also tested that allowed 1) sampling bias for the first cohort, 2) age-dependent standard deviation in length-at-age, and 3) seasonally oscillating growth to be added as additional parameters in the model. The more complex models incorporated all possible combinations of these parameters and used likelihood ratio tests to identify the model of best fit. The significance of improvement of fit within models by adding year classes was tested for significance at the 0.10 level (see Fournier et al., 1990), and significance of improvement of fit between models by adding extra parameters was tested at the 0.05 level.

The seasonal form of the von Bertalanffy equation for the length-frequency data is

$$\mu_{ja} = m_1 + (m_N - m_1)\,\frac{1-\rho^{\left[(j-1)+(t_a/12)+f(t_a)\right]}}{1-\rho^{(N-1)}},$$

where $$f(t_a) = \frac{\phi_1}{2\pi}\sin\left[2\pi\left(\frac{t_a+1}{12}-\phi_2\right)\right],$$

μ_{ja} = the mean length of fish of the j^{th} age class in the a^{th} length-frequency data set;
m_1 = the mean length of the first age class;
m_N = the mean length of the last age class;
ρ = the Brody growth coefficient;
t_α = the number of months after the presumed birth month of the fish in the a^{th} length-frequency data set;
N = the number of age classes present; and
ϕ_1 and ϕ_2 describe the amplitude and phase of the seasonal component, respectively (Fournier et al., 1990, 1991; Francis and Francis, 1992).

Comparisons of rates of growth from calcified structures and from tagging and length-frequency data

Rates of growth were estimated from aging structures and from length-frequency (both age-based) and mark-recapture (length-based) data with methods outlined in Francis (1995). The aging error model of Richards et al. (1992) that showed the best fit to the data matrix comprising two age readings from each of the three aging structures was used to determine a single age for each fish. Schnute's growth curve (case 2) was then fitted to the age-size data and this mean age-size relationship was used as a basis with which to compare the estimates of growth from the different data sets. The annual growth for the age-size data and length-frequency data was calculated as the mean size at age x minus the mean size-at-age (x+1; Francis, 1995). Annual growth at corresponding points on the size-based line was then estimated at the size the fish was at age x, as determined from the fit to the mark-recapture data obtained by using GROTAG.

Results

Structures for aging *Seriola lalandi* were collected from a total of 572 fish ranging in size from 323 to 1090 mm FL, although not all structures were collected from all fish. Although *S. lalandi* is reported to reach a total length of almost 2000 mm (1700 mm FL) and a weight of 60 kg, fish of this size are rare. In New South Wales, few fish over 20 kg (about 1200 mm FL) are caught by commercial fishermen and the largest fish recorded in surveys of amateur fishermen has been 1140 mm FL (Steffe et al.[2]). We were unable to obtain fish larger than 1100 mm FL.

All structures showed zones that could be interpreted as annuli (Fig. 1); however, zones were not interpretable in all fish. Growth zones in whole otoliths were more easily interpretable than those in sectioned otoliths (Fig. 2); the latter showed numerous striations that could rarely be interpreted. Zones in sectioned otoliths were, however, clearer in some larger fish (Fig. 2). A large number of scales had to be collected because preliminary results showed that two-thirds of fish had at least some regenerated scales. Vertebrae did not always stain well and showed pronounced ridges which reduced readability in many fish.

Validation of aging methods

Analysis of marginal increments showed different patterns among structures (Table 2). Otoliths and scales revealed that one zone was laid down per year, in August–September (otoliths) and between Decem-

[2] Steffe, A., J. Murphy, D. Chapman, B. E. Tarlington, G. N. G. Gordon, and A. Grinberg. 1996. An assessment of the impact of offshore recreational fishing in New South Wales on the management of commercial fisheries. Final Report to Fisherires Research Development Corporation, PO Box 222, Deakin West ACT 2600, Australia.

Table 2

Results of analyses of marginal increments for kingfish aged by otoliths, scales, and vertebrae. Each category is the growth of the structure, subsequent to the most recent zone, as a percentage of the previously completed zone. The percentage of fish in each category for each two-month period is shown; sample sizes are also indicated (in parentheses beside month). Only fish aged 2–4 were used for analyses. For each row, the highest percentage of fish is shown in bold.

	Category				
Month	Edge	20	40	60	80
Otoliths					
Aug–Sep (34)	**44**	35	15	0	6
Oct–Nov (149)	16	**36**	24	10	13
Dec–Jan (87)	9	7	18	24	**41**
Feb–Mar (68)	1	13	**31**	24	**31**
Scales					
Aug–Sep (0)					
Oct–Nov (181)	15	12	21	24	**29**
Dec–Jan (94)	22	**34**	21	7	15
Feb–Mar (101)	1	19	28	**34**	19
Vertebrae					
Aug–Sep (51)	8	16	16	10	**51**
Oct–Nov (173)	16	20	**24**	16	23
Dec–Jan (50)	14	12	**28**	20	26
Feb–Mar (70)	14	13	**37**	11	24

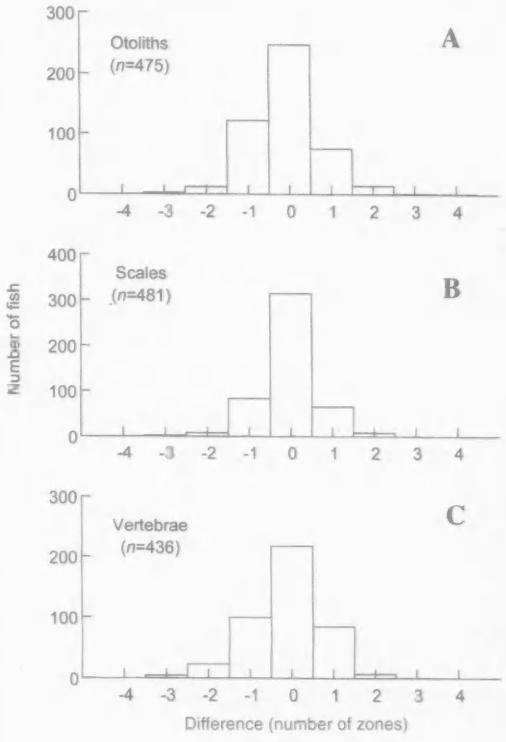

Figure 4

Differences between repeated counts of zones for three structures used to age kingfish. Each comparison represents independent counts from a single reader.

ber and January (scales; Table 2). No data were, however, obtained for scales in August–September and sample sizes were small between April and July (n=1–7 fish per month) for all structures. No clear pattern of marginal zones was observed in vertebrae (Table 2).

Precision within and among structures

Comparisons of two independent counts of zones in a structure resulted in a relatively low level of agreement (50–66%). Depending on the structure, between 92% and 96% of readings agreed within one zone (Fig. 4). Differences in counts of zones varied by up to four zones (Fig. 4). Mean coefficients of variation among counts ranged from 7.6% (scales) to 12% (otoliths).

Comparison of readings between structures showed a large amount of variation, with differences between structures varying by up to six growth zones (Fig. 5). Agreement between any two methods decreased with age, but otoliths and vertebrae had the greatest concordance in fish aged 4 and over. Fish were never assigned an age of 0 when aged with scales; fish assigned 0 or 1 with other structures were assigned an age of 1 with scales. Readings between structures agreed within one zone between 88% (between vertebrae and otoliths) and 91% (between scales and otoliths) of the time.

Estimates of aging error

Analysis of aging precision with the methods of Richards et al. (1992) showed that the estimates of assigned age were more precise for young fish (Fig. 6A). For example, with otoliths, 98% of fish with an estimated most probable age of 0 were likely to be aged as 0, whereas only 74% of fish with a most probable age of 4 were likely to be aged as 4. This precision can be compared with those obtained from other structures (e.g. scales and vertebrae; Fig. 6A). Fish aged with scales had a higher probability of being consistently assigned ages 1 and 2. Fish aged with vertebrae or otoliths, however, had a higher probability of being consistently assigned age 4, whereas there was little difference between the three structures in assigning fish to age 3 (Fig. 6A).

A more complex aging error model, with parameters that accounted for effects due to aging structures showed that fish in their first year (i.e. 0 growth zones) were likely to be overestimated with scales and vertebrae than with otoliths. Otoliths underestimated the age of fish in their first year, although this is due to the relative nature of the model because vertebrae and scales overestimated the age of these fish (Fig. 6B). Scales showed less bias in relation to the other structures for fish aged 1–4 (Fig. 6B).

Estimates of rates of growth

Patterns in growth of kingfish from NSW were obtained from Schnute's (1981) growth model fitted to the estimated most probable ages of fish calculated from the different aging structures (Fig. 7). Size-age data were best fitted by three-parameter models for otoliths, vertebrae (both case 2, see Table 1) and scales (case 3). Using the best fitting model for each structure, we estimated that the average lengths (± standard error) of fish with one growth zone were 499 (±5), 418 (±9), and 485 (±7) mm FL for otoliths, scales, and vertebrae respectively. At age 5, fish were 807 (±8), 823 (±8), and 788 (±6) mm FL for otoliths, scales, and vertebrae respectively. The maximum age of fish was 9 yr for otoliths and scales, compared to 11 yr for vertebrae (Fig. 7). Vertebrae tended to produce higher age estimates than did otoliths and scales, with 5% of fish showing greater than five growth zones in vertebrae compared with only 2% for scales and otoliths. Using a single age for each fish, we estimated an age-length key for fish sampled during the current study (Table 3). Fish in all length classes were found in more than one age class (Table 3).

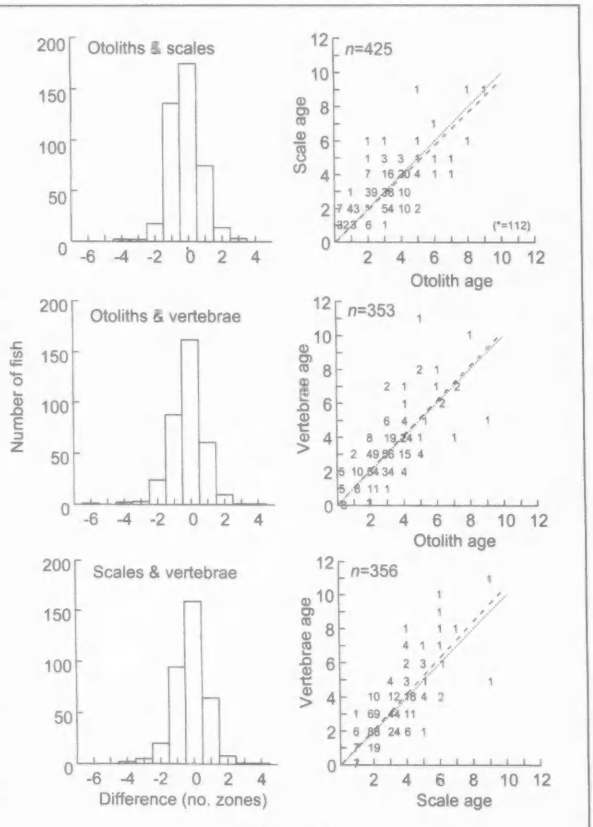

Figure 5

Counts of zones from kingfish otoliths, scales, and vertebrae compared with other aging structures. Histograms show the difference between structures, and the scatterplots enable comparisons between structures by age. In each scatterplot, the line of slope 1 (dotted line) indicates 100% agreement. The line of best fit (dashed line) is indicated with a dashed line. The sample size for each point on the scatterplots is also shown.

The different aging structures showed significant differences in mean size-at-age for some age classes. Scales showed significantly different mean size-at-age to otoliths and vertebrae for fish with one growth zone (t-tests, $P<0.05$). Otoliths and vertebrae gave similar estimates of mean size-at-age for fish with less than eight growth zones (t-tests, $P<0.05$). With the exception of fish with one growth zone, scales gave similar estimates of mean size-at-age to otoliths for all other age classes (t-tests, $P<0.05$). Although differences between scales and vertebrae were statistically significant for some age classes (fish with 4–6 growth zones), these differences were not likely to be biologically important.

Kingfish that were measured at both tagging and recapture were at large for between 0 days (i.e. recaptured the same day that they were tagged) and 5 years (Fig. 3B). Growth of recaptured fish ranged from a decrease of 350 mm to an increase of 800 mm (Fig. 3A). The frequency distribution of fish at large <30 days showed that fishermen were just as likely to underestimate the length of fish as they were to overestimate the length of fish (Fig. 3A). The mean difference in size of fish between tagging and recapture for fish recaptured within 30 days was 11.6 mm (±0.4, SE), suggesting that there was little bias in measurements between tagging and recapture. Size of fish at tagging ranged from 220 to 1200 mm, although the majority of fish were between 400 and 600 mm TL (Fig. 3C).

The best fit to the complete tag-recapture data set (model 1 in Table 4) showed a high proportion of outliers ($P=0.04$). Twenty-two fish (or 2.7%) that had absolute standardized residu-

als greater than 3 in the model 1 fit were removed from the data set. Initially, a simple three-parameter model was fitted (model 2 in Table 4), which indicated growth rates of 255 mm and 176 mm for 400-mm and 600-mm fish, respectively. The first additional parameter selected was that describing the shape of the growth curve (model 3 in Table 4). Model 3 showed annual growth rates of 270 and 140 mm. There was a significant improvement in fit when a term describing growth variability was added (model 4 in Table 4). Additional parameters (e.g. seasonal growth terms) did not result in significant improvements of fit. The best fitting model was therefore case-1 model in Table 1. Plots of standardized residuals against length at tagging, time at liberty, and expected growth increment showed no pattern (correlations were 0.022, 0.003, and 0.005, respectively) suggesting that the model was appropriate.

The best fitting model for the kingfish length-frequency data set identified five cohorts aged from 1.73 to 5.73 years (Table 5; Fig. 8). The standard deviation of the predicted length estimates for each age class increased with age. Parameters for first length bias and seasonal growth were also included in the best fitting model (Table 5; Fig. 9). Estimates of the mean length-at-age (and standard deviation) for the length-frequency data set are given in Table 5. The mean lengths and proportions of the modes predicted by MULTIFAN generally fitted the observed data (Fig. 8). There were large numbers of small fish (e.g. 1 yr) in the catch during the summer months (e.g. November and December), whereas 2-yr fish dominated the catch at other times. Small numbers of large fish (e.g. greater than 5 yr) were found throughout the year (Fig. 8). The seasonal form of the von Bertalanffy growth equation showed that the projected value of L_∞ was 1252 mm FL and the rate of change in growth increment (K) was 0.189 (Fig. 9).

Comparison of annual growth between age-based (age-length and length-frequency) and length-based (mark-recapture) data, although not strictly comparable, showed a decrease in growth with age and size of fish (Fig. 10). Estimates of annual growth were similar among the three methods for 2–4 year fish (≈550–750 mm SL) but varied by ≈50 mm for 1-yr-old fish.

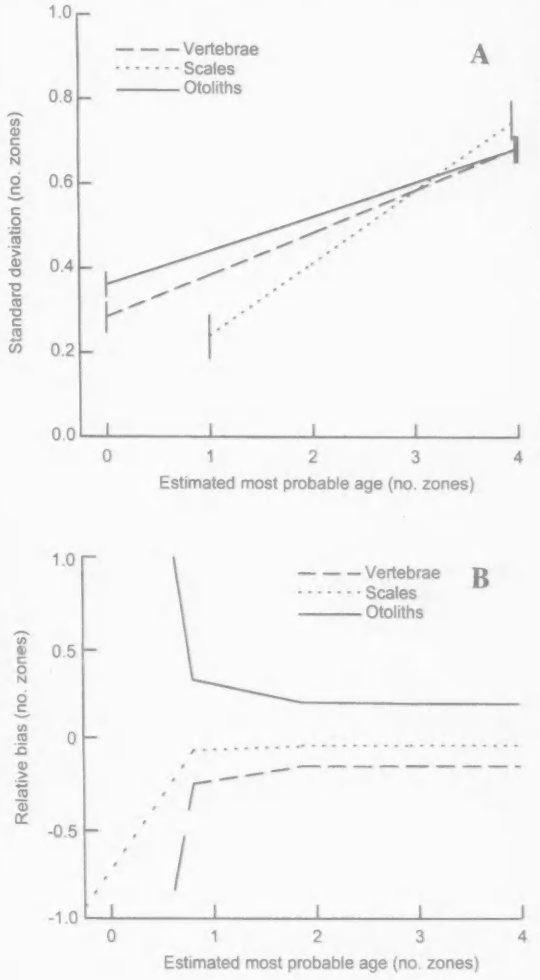

Figure 6

(**A**) Aging error versus estimated most probable age for kingfish aged with otoliths, scales, and vertebrae. Estimated most probable age was calculated separately for each structure by using the methods of Richards et al. (1992), see text for further details. Errors around the first and last ages are indicated by the vertical lines. (**B**) Relative bias versus estimated most probable age for kingfish aged by otoliths, scales, and vertebrae. Relative bias was calculated from a model that incorporated two age readings from each of the three structures.

Discussion

All structures showed patterns of growth that were, to varying degrees, quantifiable. Delineation of each zone was, however, sometimes difficult, as has been found in other studies (e.g. Brennan and Cailliet, 1989; Manooch and Potts, 1997), and the clarity of zones varied among individuals for all structures. Because pelagic fishes including *Seriola* spp. are known to be difficult to age, these results were not surprising.

To accurately reflect the age of a fish, the zones must be formed on a regular and determinable time scale.

Small sample sizes during the winter months (from April to July), due in part to small numbers of fish being taken in the fishery, made analysis of marginal increments problematic, especially for scales because samples were also not obtained in August–September. With the exceptions of otoliths and possibly scales, our data were not sufficient to confirm that only one zone was formed per year. No single category of marginal growth ever had more than 50% of fish for any structure. A previous study (Mitani and Sato, 1959) also found that fish (*Seriola quinqueradiata*) collected in any one time period showed a wide range of marginal growth conditions. Growth zones on the edge of the otoliths of *S. dumerili* were also found over five months of the year (Manooch and Potts, 1997). The wide range of marginal growth patterns in our study may in part be due to grouping of samples into two-month intervals or because fish from three age classes (2–4 growth zones) were used in analyses. Fish from different age classes have previously been shown to lay down zones at slightly different times of year (e.g. Francis et al., 1992).

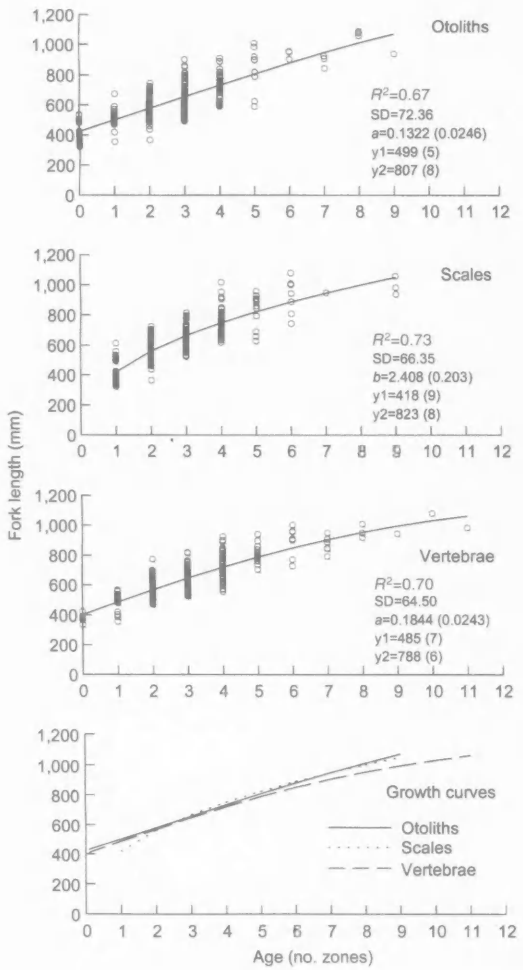

Figure 7

Relationship between fork length and age for the different structures used to age kingfish (**A–C**) and (**D**) comparison of the three growth curves. The growth curves were calculated by using Schnute's growth model. R^2, overall standard deviation (SD), and the parameters (standard error) describing the growth model are shown. y_1 is size at age 1, y_2 is size at age 5, a and b are parameters that describe the shape of the curve. The formulae for the growth curves are found in Table 1.

Analysis of marginal increments often provides only partial validation of age estimates because older fish with slower growth often do not show seasonality in formation of zones. A method should not be considered accurate until all reported ages are validated (Beamish and McFarlane, 1983). Validation of age estimates in older fish will require a mark-recapture study, but further work on validation in younger fish may use a variety of approaches (e.g. length-frequency analyses if cohorts are easily recognized, mark-recapture etc). In the present study, few tagged fish were at large more than a year (Fig. 3B), which suggests that many fish would have to be tagged in a mark-recapture study to recover sufficient fish to make this approach feasible.

There have been few validation studies on *Seriola* spp. and all have involved analysis of marginal increments. Mitani and Sato (1959) have suggested that one zone is laid down each winter in opercular bones of *S. quinqueradiata* and Baxter (1960) found that zones are formed between November and January in scales of *S. lalandi* (formerly *dorsalis*). In otoliths of *S. lalandi* opaque zones appear to be laid down in August or September. Timing of zone formation in scales and vertebrae was more variable and may differ between structures because processes involved in deposition vary among bone, scales, and otoliths (Simkiss, 1974).

Precision of aging estimates

Exact agreement among age estimates for each structure was generally poor; agreement within one zone was reasonable for all structures. The use of percent agreement (i.e. percent of fish aged alike between sets of multiple readings) has been criticized because it fails to take into account the range of year classes of fish and therefore can be used only for age-specific comparisons (Kimura

Table 3

Kingfish age-length (FL, mm) distribution for fish collected from New South Wales, Australia, between August 1995 and July 1996. Shown are the number of fish and the percentage of the length class (in parentheses). Ages were estimated from the aging error model that showed the best fit to the data matrix comprising two age readings from each of the three aging structures where fish had less than five growth zones or by randomly selecting one of the six age readings where fish had five or more growth zones.

	Age (yr)										
Length class	0	1	2	3	4	5	6	7	8	9	Total
300–350	4 (66.7)	1 (16.7)	1 (16.7)								6
351–400	11 (47.8)	7 (30.4)	5 (21.7)								23
401–450	4 (40.0)	4 (40.0)	2 (20.0)								10
451–500		11 (34.4)	19 (59.4)	2 (6.3)							32
501–550		11 (10.6)	85 (81.7)	8 (7.7)							104
551–600		1 (1.1)	67 (71.3)	26 (27.7)							94
601–650			54 (50.9)	51 (48.1)	1 (0.9)						106
651–700			14 (19.2)	52 (71.2)	6 (8.2)	1 (1.4)					73
701–750			5 (13.2)	16 (42.1)	14 (36.8)	2 (5.3)	1 (2.6)				38
751–800			1 (3.1)	9 (28.1)	16 (50.0)	4 (12.5)	1 (3.1)	1 (3.1)			32
801–850				3 (21.4)	4 (28.6)	4 (28.6)	3 (21.4)				14
851–900					2 (62.5)	5 (62.5)	1 (12.5)				8
901–950					1 (18.2)	2 (18.2)	4 (36.4)	3 (27.3)		1 (9.1)	11
951–1000							1 (33.3)		1 (33.3)	1 (33.3)	3
1001–1050						1 (33.3)	1 (33.3)		1 (33.3)		3
1051–1100									1 (33.3)	2 (66.7)	3
N	19	35	253	167	44	19	12	4	3	4	560

Table 4

Log likelihood function values, growth parameter estimates, and standard errors (model 4 only) for kingfish (*Seriola lalandi*) tagging data. * indicates that parameters were held fixed. Standard errors of parameter estimates were estimated from simulated data (n=100 simulations). Growth rates are shown for 400 mm (g_{400}) and 600 mm (g_{600}) TL fish. The best model fit (model 4) is the case-1 model from Table 1.

Parameter		Model 1	Model 2	Model 3	Model 4	SE
Log-likelihood		2890.67	2797.80	2735.35	2706.21	
Mean growth rate	g_{400} (mm)	263.8	255.3	269.6	260.3	8.1
	g_{600} (mm)	132.1	176.4	140.1	131.1	7.3
Seasonal variation	u (year)	0.164	0*	0*	0*	
	w (year)	0.706	0*	0*	0*	
Growth variability	v	0.397	0*	0*	0.40	0.045
SD measurement error	s (mm)	66.9	82.1	75.8	66.4	1.70
Outlier contamination	P	0.037	0*	0*	0.000	
Curvature in model	b	5.47	0*	5.21	5.66	0.568
Sample size	n	816	794	794	794	

and Lyons, 1991). More recently, the belief that percentage agreement is inappropriate has been questioned. Although it is acknowledged that percent agreement is not interpretable as a property of the species or stock, it is thought to be more intuitive than other methods (Hoenig et al., 1995). Coefficient of variation (CV) is thought to adjust for the absolute age of the fish and therefore is frequently used to make comparisons among species of varying ages. Kingfish had values of CV within those of previous studies, but at the higher end (present study 7.6–12% versus other species 3.2-12.9% [Kimura and

Lyons, 1991]) suggesting that *S. lalandi* was a more difficult species to age. For kingfish, scales (7.6%) had lower values of CV than did otoliths (12%) and vertebrae (11%). The lowest CV values were for structures where no fish were in their first year (e.g. scales), and the highest values were for structures where fish were aged as in their first year (e.g. otoliths and vertebrae). Similarly, Kimura and Lyons (1991) found that the CV was highest for species in which 1-year age classes were present and lowest where the youngest age classes were 2 or 3 years. Coefficient of variation therefore depends on the minimum age of fish and we suggest that its use be limited to comparisons where fish have the same range of ages. Such indices, if averaged over all fish, are also thought to simplify the data because any trends that might occur with age are ignored (see Hoenig et al., 1995). Precision of aging decreased with age of fish for all structures, suggesting that estimates of precision should not be averaged over all age classes. We believe that the methods of Richards et al. (1992) give a better indication of aging error, and therefore precision, than did methods that summarized over all age classes.

Table 5

Estimated parameters from the MULTIFAN analysis of the length-frequency data, with predicted fork lengths (FL) and standard deviations (SD) of lengths at age.

Parameter		Estimated value
Number of cohorts (N)		5
von Bertalanffy K		0.189/year
von Bertalanffy L_∞		1,252 mm
Brody's rho (ρ)		0.828
First length (m_1)		349.5 mm
Last length (m_N)		828.4 mm
Age of first year class		1.73 years
Mean length sampling bias		26.13 mm
Seasonal growth amplitude (ϕ_1)		0.611
Seasonal growth phase (ϕ_2)		0.087 years
Mean SD		44.4 mm
Ratio of first to last SD		1.897
Age	Predicted FL (mm)	Length-at-age SD
1	349.5	32.2
2	505.0	39.7
3	633.7	47.1
4	740.2	54.3
5	828.4	61.1

Length at age

Estimates of mean size-at-age calculated from growth models suggested that the resulting growth curves from otoliths, scales, and vertebrae were similar for all but the youngest age class. Although other aging studies on *Seriola* spp. have calculated average length-at-age (e.g. Mitani, 1955; Mitani and Sato, 1959), few have fitted models to the data (but see Baxter, 1960; Manooch and Potts, 1997). Growth models from all aging structures were within the range of growth of *Seriola* spp. described elsewhere (e.g. Mitani, 1955, 1958; Mitani and Sato, 1959; Baxter, 1960; Murayama, 1992).

Further research needs to focus on the position of the first zone in all structures because this may contribute to differences in the shape of the growth curves between structures. No fish were found to be in their first year (i.e. 0) when aged with scales, but fish were found to be in their first year when aged with otoliths and vertebrae. There are also differences in estimated mean size between scales and both otoliths and vertebrae for fish with one growth zone, which is also likely to be due to the detectability of the first zone. Either scales lay down a false first zone or the first zone is not detected in otoliths and vertebrae, possibly because it is close to the edge of the structure. Collections of fish from recruitment over a 12-month period and sampling of all structures may help elucidate the position of the first zone.

Although, it is well known that age estimates from scales are inaccurate once growth becomes asymptotic (Beamish and McFarlane, 1987), scales did not appear to underestimate ages of kingfish in relation to otoliths in the present study but may have underestimated ages of older fish in relation to vertebrae (e.g. Fig. 5). In a previous study on *S. lalandi*, spaces between circuli became increasingly narrow after the seventh year, so that it was impossible to differentiate between one year's growth and the next (Baxter, 1960). Few fish, however, had greater than seven growth zones in the current study.

Many studies have found that sectioned otoliths are preferable to whole otoliths for aging because examination of whole otoliths does not take into account the asymmetric deposition of material (Campana, 1984). After a certain age, deposition may thicken the otolith and growth along the anteroposterior axis may decline; therefore only transverse sections would reveal recently formed growth zones (Beamish, 1979). Growth zones on whole otoliths were interpretable for aging kingfish, but zones could rarely be interpreted on sectioned otoliths. This is unusual because in many studies, sectioned otoliths have been found to give more precise and accurate estimates of age than whole otoliths (e.g. Beamish,

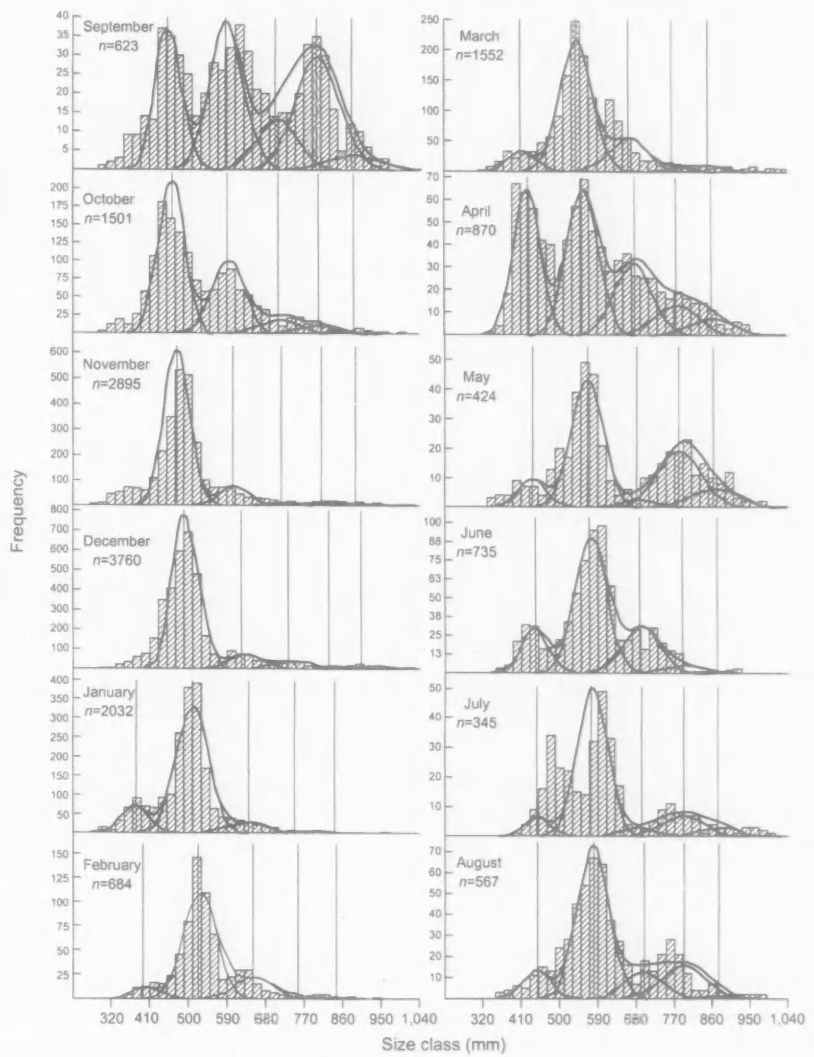

Figure 8

Observed length-frequency distributions for kingfish data (shaded histograms), showing the fit of the MULTIFAN model (see Table 5 for model details). Estimated frequencies for each age class (inner smoothed curves) and for the sum of all age classes (outer smooth curve) are shown. Vertical lines represent the estimated mean lengths-at-age in each sample.

1979; Campana, 1984). Manooch and Potts (1997) have used sectioned otoliths to age *S. dumerili* but commented that age and growth determinations were very difficult. Measurements could only be made on 48% of samples and zones could only be counted on 71% of samples and thus may have biased estimates of growth in their study. Whole otoliths were examined in their study solely to determine the plane of sectioning (Manooch and Potts, 1997). Because whole otoliths may underestimate age of large fish (e.g. Beamish, 1979; Campana, 1984), it may also be useful to look at transverse sections of otoliths of kingfish for extremely large fish (>20 kg).

Comparison of age- and length-based data

Although not strictly comparable (see Francis, 1988a, 1995), estimates of growth from length-frequency,

age-length (both age-based data), and tagging data (length-based) showed agreement for fish aged 2–4 years but varied for fish with one growth zone. Differences in rates of growth were greater for younger fish than for older fish and may have been caused by inaccuracies in aging, influence of tagging on growth (e.g. McFarlane and Beamish, 1990), within- or between-year differences, and variations in year-class strength. Although estimates of growth from tagging data provide some indication that age-length data may be reasonable, they should not be used as a means of validation (see Francis, 1988a).

Tagging data also suggest that *S. lalandi* in New South Wales has greater annual growth than the same species in New Zealand and the United States (Baxter, 1960; Holdsworth[3]). For *S. lalandi* in New South Wales, annual growth rates of 144 mm were found for 500-mm-FL fish, compared with 93 mm (New Zealand) and a range of 34–109 mm (US) for similar size fish. In New Zealand, annual growth of 44 mm was found for 1000-mm-FL fish, which is within the range found in the United States (19–70 mm). Few large fish were tagged in New South Wales, preventing estimates of annual growth at this larger size.

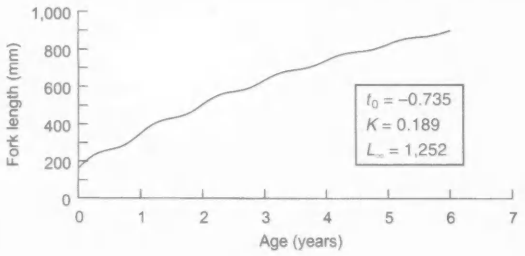

Figure 9

MULTIFAN growth curve for the length-frequency data. A model incorporating seasonal growth is shown. Values of t_0, K, and L_∞ (mm) are shown.

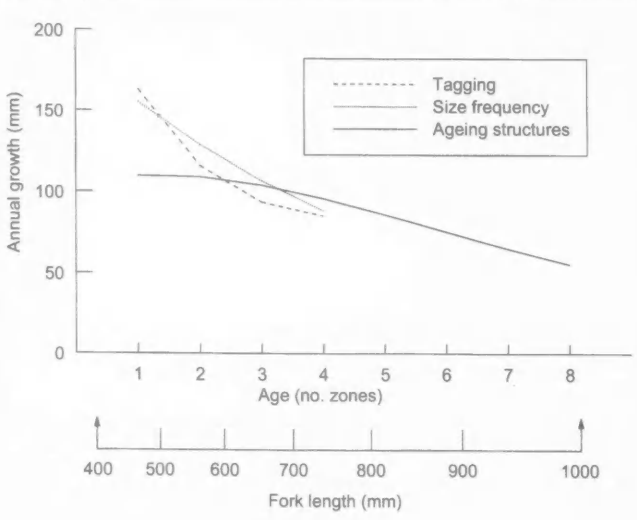

Figure 10

Comparison of rates of annual growth for kingfish estimated from (**A**) aging structures, (**B**) length-frequency (both age-based) and (**C**) mark-recapture (length-based) data. The mean length at any age is aligned with the corresponding point on the age axis; this was calculated from age-size data obtained from the aging structures.

Practicalities of aging kingfish

With the exception of dorsal spines, which did not appear useful for aging kingfish, only scales can be easily collected without altering the market value of the fish because *Seriola lalandi* are preferentially sold whole in NSW. Scales showed similar estimates of mean size-at-age to otoliths for all age classes except fish with one growth zone, but their use in aging kingfish can only be recommended with caution until the position of the first growth zone is better understood. The usefulness of otoliths and vertebrae may be limited by the cost of fish, but, if possible, collections of at least one of these structures should be made. The similarity of age estimates among structures suggests that, if validations are possible, kingfish may be aged reliably.

Acknowledgments

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[3] Holdsworth, J. C. 1997. Ministry of Fisheries, 17 Keyte Street, Kensington, private Bag 9013, Whangarei, New Zealand. Unpubl. data.

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Age, growth, mortality, and reproduction of vermilion snapper, *Rhomboplites aurorubens*, from the eastern Gulf of Mexico

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Abstract.—Fishing pressure on vermilion snapper, *Rhomboplites aurorubens*, in the Gulf of Mexico has increased since the mid-1970s, and populations are thought to be overfished. We sampled 858 vermilion snapper (192–585 mm TL) from the eastern Gulf of Mexico during 1995 and 1996 to assess their age structure, growth, mortality, spawning season, size and age at maturity, and batch fecundity. The lengths of males and females in our samples were not significantly different, and the overall sex ratio was not significantly different from 1:1. Marginal-increment analysis indicated that one opaque zone is formed on vermilion snapper otoliths during the late spring to early summer of each year. Ages ranged from 1 to 13 years, and von Bertalanffy growth models for males and females were not significantly different. Von Bertalanffy growth model parameters were L_∞ = 298 mm TL, K=0.25/yr, and t_0=–3.9 years for all aged fish. Growth rates in our study were lower than those in previous studies of Gulf of Mexico vermilion snapper, perhaps the result of recent changes in fishing selectivity. Pooled estimates of total instantaneous mortality were 0.480/yr based on recreational landings data and 0.489/yr based on commercial landings data. Most females and all males examined were mature. At 200 mm TL, 90% of the females we examined were mature. Vermilion snapper are summer spawners, and ripe females were caught from May to September. Batch fecundity ranged from 5535 to 22,811 oocytes and was positively correlated with fish weight (batch fecundity=317 × (whole weight) – 3.1624×10^4, r^2 = 0.55).

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Fish. Bull. 97:828–841 (1999).

The vermilion snapper, *Rhomboplites aurorubens*, is a small, subtropical lutjanid that occurs from North Carolina to Rio de Janeiro but is most abundant off the southeastern United States and in the Gulf of Campeche (Vergara, 1978). In the Gulf of Mexico (GOM), vermilion snapper are usually found near hard bottom areas off the west-central Florida coast, the Florida Middle Ground, and the Texas Flower Gardens (Smith et al., 1975; Smith, 1976; Nelson, 1988). Faunal surveys in the South Atlantic Bight (SAB) have indicated that vermilion snapper are most common over inshore live-bottom habitats and over shelf-edge, rocky-rubble, and rock-outcrop habitats (Grimes et al., 1977, 1982; Barans and Henry, 1984; Chester et al., 1984; Sedberry and Van Dolah, 1984).

Vermilion snapper are an important component of the reef fish fishery on the west coast of Florida. In 1995 and 1996, total commercial landings of vermilion snapper on Florida's west coast was 1.6 million pounds and had an estimated dockside value of $4.5 million (Marine Fisheries Information System[1]). Over the same period, 1.8 million vermilion snapper were landed by anglers in Florida (MRFSS[2]). Charter boats or headboats accounted for most (90%) of the angler-caught fish (Goodyear and Schirripa[3]; Schirripa[4]).

The Gulf of Mexico stock of vermilion snapper is showing signs of being overfished. Schirripa[4] reported in an analysis of GOM vermilion snapper landings data that 1) overall landings were declining, 2) the fishery was consolidating to the most productive fishing areas, 3) the mean size of fish in the commercial catch was decreasing, 4) the catch per unit of effort was decreas-

[1] Marine Fisheries Information System. 1997. Florida Department of Environmental Protection, 100 8th Avenue S.E., St. Petersburg, FL. Unpubl. data.

[2] MRFSS (Marine Recreational Fishery Statistics Survey). 1997. Fisheries Statistics Division, National Marine Fisheries Service, Department of Commerce, Silver Springs, MD. Unpubl. data.

[3] Goodyear, C. P., and M. J. Schirripa. 1991. A biological profile for vermilion snapper with a description of the fishery in the Gulf of Mexico. Miami Laboratory, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL. Contribution rep. MIA-90/91-78.

[4] Schirripa, M. J. 1996. Status of the vermilion snapper fishery of the Gulf of Mexico: assessment 3.0. Miami Laboratory, Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Miami, FL. Contribution rep. MIA-95/96-61.

ing, and 5) the estimated number of age-1 fish in the population was declining. Goodyear and Schirripa[3] also noted that large differences in estimates of length-at-age and estimates of fecundity made it difficult to assess confidently conditions of the stock by using standard assessment models.

Existing age and growth data for this species in the GOM are inadequate and dated. Zastrow (1984) and Nelson (1988) used scales to age GOM vermilion snapper collected in the early 1980s. The maximum age reported was 7 years. However, using scales to determine age has proven to be problematic. Studies in the SAB have shown that as age increases, the readability of the scales decreases (Grimes, 1978; Collins and Pinckney, 1988). Barber (1989) used whole otoliths and scales to age GOM fish and was able to count up to 18 rings in scales and 26 rings in whole otoliths. Although he did not directly compare ages from both structures, his scale- and otolith-based estimates of length at age and growth were very different. In addition, his attempt to validate whole-otolith-based ages was unsuccessful.

Growth of vermilion snapper may be affected by changes in fishing. Zhao et al. (1997) found that mean and predicted sizes-at-age of SAB fish had declined between 1979 and 1993 and associated this change with size-selective fishing. They suggested that fishing is removing faster-growing fish from the population and may have genetic or physiological consequences in the life history of this species.

Information on the reproductive biology of vermilion snapper in the GOM is limited. Sex ratio appears to be dependent on location. Sex ratios from the GOM and Puerto Rico are approximately 1:1 (Boardman and Weiler, 1979; Zastrow, 1984; Collins[5]) although Nelson (1988) reported that males outnumbered females 1.2:1. In the SAB, females consistently outnumbered males, and sex ratios ranged from 1.6:1 to 1.7:1 (Grimes and Huntsman, 1980; Collins and Pinckney, 1988; Cuellar et al., 1996; Zhao and McGovern, 1997). Nelson (1988) examined spawning period, fecundity, and sex ratios of fish caught in the western GOM. His results were similar to findings reported for the SAB (Grimes and Huntsman, 1980; Cuellar et al., 1996). In both regions, spawning occurs during the summer and early fall. Nelson (1988) estimated that vermilion snapper batch fecundities in the GOM range from 61,600 to 392,000 eggs. Fecundity has been found to have a positive relationship with fish size (Grimes and Huntsman, 1980; Nelson, 1988; Cuellar et al., 1996). Vermilion snapper are thought to spawn in aggregations. Boardman and Weiler (1979) and Grimes and Huntsman (1980) found large numbers of fish in the same reproductive state in single collections.

Basic life-history information is needed to properly assess vermilion snapper stocks in the GOM. Accurate ages are needed to develop age-length keys, develop growth models, and estimate total mortality. In addition, the annual periodicity of ring deposition in otoliths has not been validated in the GOM. With the increasing reliance on estimates of spawning-potential ratios to describe a stock's condition, information on maturation schedules, sex ratios, and size-specific fecundities are also needed. The purpose of this study was to accurately age eastern GOM vermilion snapper to develop age-length keys, develop growth models, construct catch curves for deriving estimates of total mortality, and to describe the reproductive biology of this species.

Methods

Eastern GOM vermilion snapper were sampled from October 1995 to September 1996. Samples were obtained from headboat fishermen, commercial catches, and a Florida Department of Environmental Protection trawl survey. Total length (TL), fork length (FL), and standard length (SL) were measured to the nearest millimeter. Whole weight or gutted weight (or both) were measured to the nearest gram. The relationships between lengths and $\log_{10}$-transformed total lengths and weights were determined by least-squares regression (SAS Institute, Inc., 1985). Male and female regression lines of $\log_{10}$-transformed total lengths and weights were compared by using analysis of covariance (Snedecor and Cochran, 1971).

Thin sections of sagittae (hereafter referred to generally as otoliths) were used to determine the ages of fish. Otoliths were removed and stored dry in culture wells. The left otolith was serially sectioned across its anterior–posterior midpoint at 0.5-mm intervals by making a transverse cut with an Isomet diamond saw. Mounted sections were placed on a black field, illuminated with reflected light, and examined with a binocular dissecting microscope. The magnified images of otolith sections were transmitted by means of video camera to a video monitor and were analyzed with a computer-driven data-acquisition software package (Optimas Corp., 1996). The number of opaque zones and the radial measurements from the core to the last opaque band and to the edge of the otolith (otolith radius, Fig. 1) were recorded. Marginal increments were measured as the distance between the last opaque band and the edge of the otolith.

[5] Collins, A. 1997. Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., 3500 Delwood Beach Road., Panama City, FL 32407. Personal commun.

To determine the precision of vermilion snapper otolith opaque zone counts, otoliths collected during the first four months of sampling (n=200) were read independently by two investigators. After the first reading, readers examined the sections together and compared counts to form a consensus about what constituted an opaque zone. The two readers then re-examined the sectioned otoliths independently, and counts were compared again. Because agreement between readers was 100%, one reader read the remaining otoliths to determine age. Each of the remaining otolith sections was read three times, and opaque zone counts were accepted for ages only if at least two of the three separate readings were the same. To validate annulus periodicity, marginal increments and their medians were plotted by month for each age and compared for consistent temporal patterns.

Age in years was estimated as the number of opaque zones. Therefore, length at age included any growth that occurred after the last opaque ring was formed. Mean length at age was calculated for males, females, and all aged fish. Age and observed length data were fitted to a von Bertalanffy growth model by using a nonlinear regression (SAS Institute, Inc., 1985). Growth curves were fitted separately for males, females, and all aged fish. The estimated parameters for male and female curves were compared by using likelihood-ratio tests (Kimura, 1980; Cerrato, 1990). We calculated an adjusted r^2 for the resulting curves by using methods described by Helland (1987).

We used age-frequency data from this study to estimate mortality rates from the commercial and recreational length data. Because the numbers of vermilion snapper measured in fishery sampling programs were low, we pooled the most recent years where data were available. Length data from commercial landings were obtained from the TIPS[6] from 1992 to 1994, and in 1996. Length data from recreational landings were obtained from the MRFSS[2] and pooled for years 1990–96. Instantaneous mortality and survivorship were estimated by the Chapman-Robson method (Youngs and Robson, 1978). Age at full recruitment was estimated from the catch curve as the next oldest age from the age with the greatest catch.

Reproductive analyses were based on gonad weights and a histological examination of gonadal tissue. Whole gonads were weighed to the nearest 0.1 g, fixed in 10% buffered formalin for approximately one week, rinsed in water, and then transferred to 70% ethanol. A sample was taken from the middle of the pre-

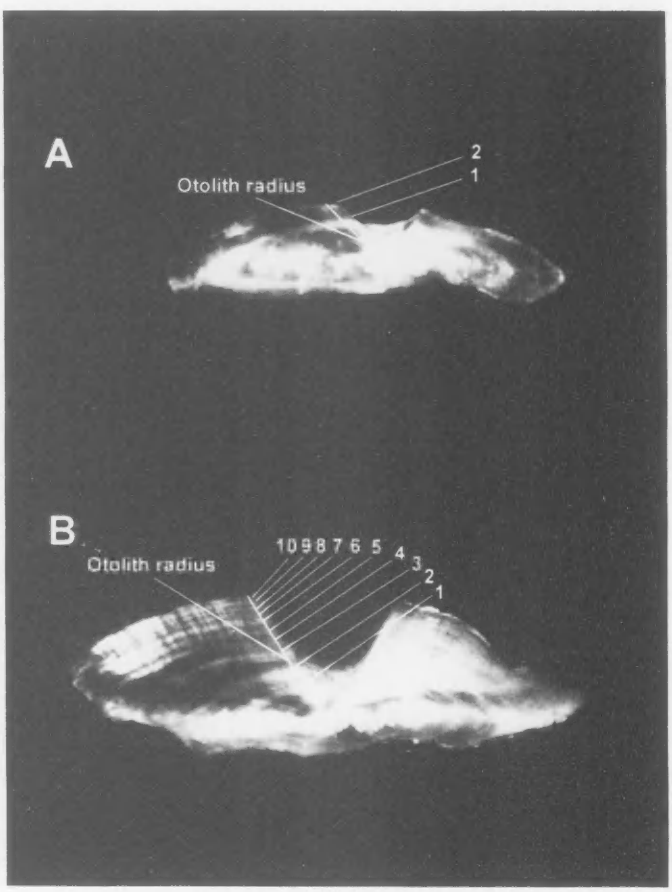

Figure 1

Sectioned saggitae from (**A**) a 2-year-old (204-mm-TL) and (**B**) a 10-year-old (184-m-TL) vermilion snapper. Both fish were caught in the eastern Gulf of Mexico in July 1996.

[6] TIPS (Trip Interview Program). 1997. Florida Department of Environmental Protection, 100 8th Avenue, S. E., St. Petersburg, FL. Unpubl. data.

Table 1
Gonad development classes for vermilion snapper.

Class	Ovary	Testes
Immature	Only primary growth oocytes present.	Spermatogonia and spermatocytes in the central lobules; no tailed sperm in the lumen of the lobule.
Resting	Primary growth oocytes and atretic bodies present.	Mostly spermatogonia and spermatocytes in the central lobules. Free spermatozoa in the lumen of the lobule, and brown bodies (Grier, 1987) may be present.
Early developing	Primary growth and cortical alveoli (yolk vesicle) oocytes present. Atretic bodies may be present.	
Developing	Primary growth, cortical alveoli, and vitellogenic oocytes present.	Mostly spermatocytes and spermatids in the central lobules, free spermatozoa in the lumen of the lobule.
Ripe	Primary growth, cortical alveoli, vitellogenic, and late-stage vitellogenic or hydrated oocytes present. Postovulatory follicles (POFs) may be present.	Mostly spermatozoa found in the central lobules and in the lumen of the lobule.
Spent	Primary growth oocytes present. Possibly some cortical alveoli oocytes present. Vitellogenic oocytes undergoing massive atresia.	Few free spermatozoa in the lumen of the lobule; early stages of spermatogenesis in the peripheral lobules.

served gonad and embedded in paraffin. We cut a 5.0-μm section from the sample, stained it with Harris's haematoxylin, counterstained it with eosin (Humason, 1972), and examined it under a compound microscope to determine sex and gonad developmental state. In addition, the frequency of oocyte developmental stages (including atretic bodies and postovulatory follicles) was tabulated for approximately 300 oocytes from each ovary by using a computer-driven data-acquisition software package (Optimas Corp., 1996). Gonadal development classes (Table 1) were determined by using modified classification schemes developed from West (1990) and Wallace and Selman (1981) for females and from Hyder (1969) for males.

Reproductive seasonality was determined by examining the monthly changes in gonad classes, the monthly distribution of oocyte stages, and the monthly changes in the gonadosomatic index (GSI). The GSI was calculated by the following equation:

$$GSI = \textit{gonad weight}/(\textit{whole weight} - \textit{gonad weight}).$$

If whole weight was not available, it was estimated from TL. Batch fecundity was estimated by counting hydrated oocytes following the gravimetric method described by Hunter et al. (1985). The relation between fish weight and batch fecundity was examined for a significant correlation by means of least-squares regression analysis (SAS Institute, Inc., 1985).

Results

Collections

We sampled 858 vermilion snapper that ranged from 192 to 585 mm TL. Most fish (87%) were between 201 and 325 mm TL. Relationships between lengths, between lengths and weights, and between weights are seen in Table 2. Male and female data were pooled for the weight-length relationship because no significant difference was found between slopes and y-intercepts of sex-specific regression equations (analysis of covariance, P=0.47 and 0.08, respectively). Most fish came from the recreational fishery (n=661) and ranged in length from 192 to 400 mm TL (Fig. 2). Fish from the commercial fishery (n=168) ranged from 225 to 585 mm TL. The mean length of recreationally caught fish (256 mm TL, SE=29) was significantly less than the mean length of commercially caught fish (324 mm TL, SE=90; t-test, P<0.001). The length-frequency distributions for commercially and recreationally caught fish were significantly different (χ^2=216, df=5, P<0.001). Fish obtained from the trawl survey (n=27) were small and ranged in length from 205 to 253 mm TL.

The mean length of males (256 mm TL, SE=4) was not significantly different from that of females (261 mm TL, SE=3; t-test, P=0.315). Males (n=392) ranged in length from 199 to 585 mm TL and females (n=430) from 192 to 518 mm TL (Fig. 2). The overall sex ratio of males to females was 1:1.1 and was not signifi-

Table 2

Linear relationships ($Y=a+bX$) between length and length, length and weight, and weight and weight for vermilion snapper from the eastern Gulf of Mexico. SL is standard length (mm); FL is fork length (mm), TL is total length (mm); WT is whole weight (gm); GWT is gutted weight (gm). n is the number of fish sampled, and standard error is in parentheses.

Y	X	n	a	b	r^2
SL	FL	857	7.5 (0.8)	0.82 (0.003)	0.99
SL	TL	869	10.5 (1.0)	0.72(0.004)	0.98
FL	SL	857	–5.5 (1.1)	1.20 (0.005)	0.99
FL	TL	854	3.4 (0.6)	0.88 (0.002)	0.995
TL	SL	869	–8.4 (1.4)	1.36(0.007)	0.98
TL	FL	854	–2.6 (0.6)	1.13 (0.003)	0.995
WT	GWT	89	–11.8(2.3)	1.15 (0.012)	0.99
$\log_{10}$WT	$\log_{10}$TL	646	–4.60(0.084)	2.87 (0.035)	0.91
$\log_{10}$GWT	$\log_{10}$TL	170	–5.01(0.05)	3.03(0.02)	0.99

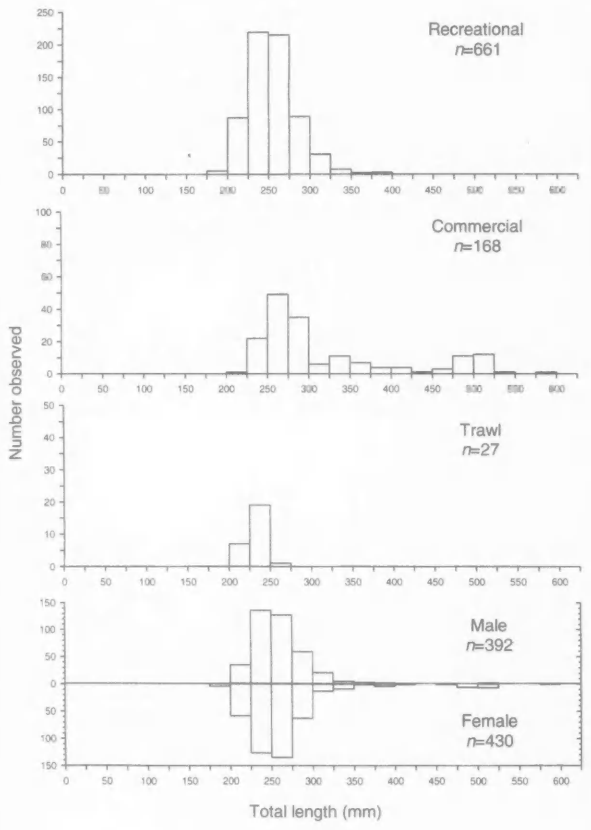

Figure 2

Total lengths of vermilion snapper from the eastern Gulf of Mexico by sampling source and by sex.

cantly different from 1:1 (χ^2=1.175, df=1, P>0.05). Seasonal sex ratios based on three-month intervals (December–February, March–May, June–August, September–November) ranged from 1:1 to 1:1.2 and were not significantly different from 1:1 (χ^2 =0.017 to 1.045, df=1, P>0.05).

Age and growth

Under reflected light, alternating opaque (white) and translucent (dark) zones were evident on vermilion snapper otoliths (Fig. 1). Two readers examined a subsample of 200 otoliths, and 57% of their readings were in agreement. Most of the disagreements (82.6%) differed by only one opaque zone. A second independent reading of the subsample by the two readers resulted in complete agreement (100%). Of 858 sectioned otoliths examined, 841 (98%) could be assigned ages. Of the otoliths that could be aged, measurements for marginal-increment analyses could not be made for 50 individuals (5.9%) because of broken or occluded areas along the otolith radius.

Analyses of marginal-increment data for fish ages 2 to 10 suggested that opaque zones were formed once a year during the late spring to early summer (Fig. 3). During this time, the widest increments (opaque zone formation was imminent) and the narrowest increments (opaque zone formation was just completed) were present. In addition, monthly median marginal increments for ages 2 to 10 had a consistent yearly pattern of high me-

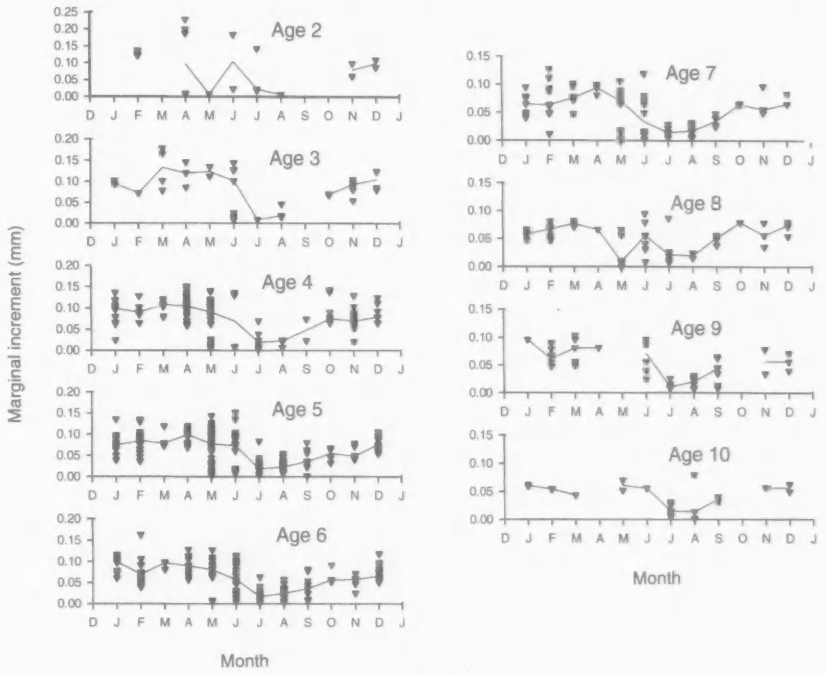

Figure 3

Marginal increments from sectioned otoliths of vermilion snapper ages 2–10 years from the eastern Gulf of Mexico. Median monthly increments are identified by the solid line.

dian values from January to May and low values in July and August (Fig. 3).

Ages ranged from 1 to 13 years. Most males (74%) and females (77%) were found to be between ages 4 and 7 (Fig. 4). Initial growth of vermilion snapper was rapid, and fish attained a mean length of 211 mm TL during their second year (age 1, Table 3). However, subsequent increases in length were low (<33 mm). Likelihood ratio tests did not show a difference between the male and female von Bertalanffy growth models (χ^2=0.92, df=3, P>0.5). The estimated von Bertalanffy growth parameters (standard error) for all aged fish (n=841) were L_{∞}=298(5.0), K=0.25 (0.04), and t_0=–3.9 (0.85). Predicted lengths at age were similar to mean lengths at age (Table 3; Fig. 5); however, because of high variability in length-at-age data, the correlation coefficient for estimated growth was low (adjusted r^2=0.26), suggesting that age is not a good predictor of length.

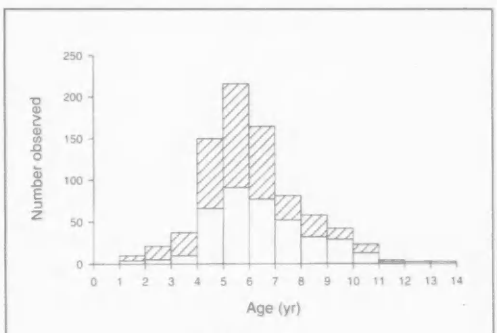

Figure 4

Age distribution of male (open) and female (hatched) vermilion snapper from the eastern Gulf of Mexico.

Mortality

Catch length-frequency data were transformed into age frequencies by using age-length keys constructed from our ages. Full recruitment into both the recreational and commercial fisheries occurred at age 6. Survivorship (standard error) estimates determined by using the Chapman-Robson method were 0.619 (0.0002) and 0.613(0.0001), respectively. Instantaneous mortality estimates (Z=–ln survivorship) were

Table 3

Mean empirical and predicted total lengths (mm TL) of female, male, and all vermilion snapper sampled from the eastern Gulf of Mexico. Standard error is in parentheses, and n is number of fish examined.

	Female			Male			All Fish			
Age	n	Mean empirical	Range	n	Mean empirical	Range	n	Mean empirical	Range	Predicted
1	6	214(13.1)	195–225	4	207(4.6)	202–212	11	211(10.1)	195–225	210
2	16	224(16.3)	200–255	5	221(13.4)	208–243	21	223(15.4)	200–255	229
3	27	249(24.7)	200–302	10	253(36.1)	225–347	37	250(27.8)	200–347	245
4	83	253(41.9)	202–518	66	245(23.8)	199–322	154	253(41.5)	199–518	257
5	124	267(60.5)	192–518	91	262(41.5)	215–505	225	270(60.8)	192–518	266
6	88	275(60.1)	205–515	76	262(29.7)	218–385	171	274(56.9)	205–515	273
7	29	263(23.7)	223–340	52	259(21.0)	225–315	85	267(43.1)	223–502	278
8	26	294(67.7)	235–500	32	270(14.8)	241–300	59	282(48.1)	235–500	283
9	13	277(21.8)	250–333	29	288(63.6)	325–585	45	293(64.4)	235–585	286
10	10	294(38.1)	267–397	13	295(69.6)	240–515	24	294(55.7)	240–515	289
11	2	281(8.5)	275–287	2	313(40.3)	284–341	4	297(29.9)	275–341	291
12				2	271(0)		2	271(0)		292
13				2	284(32.5)	261–307	3	304(42.1)	261–345	294

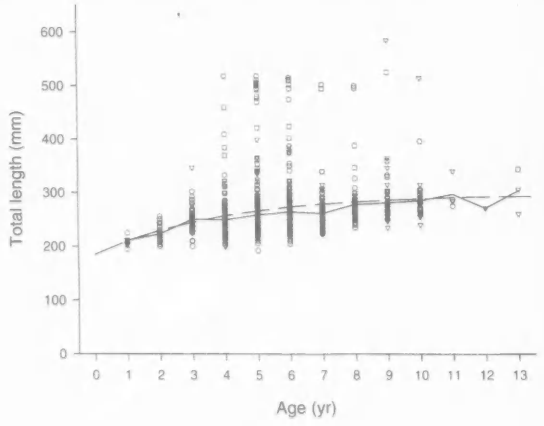

Figure 5

Total length at age, mean length at age (solid line), and predicted length at age (dashed line) for vermilion snapper from the eastern Gulf of Mexico. Circles = females, triangles = males, and squares = unknown sex.

0.480 for the recreational fishery and 0.489 for the commercial fishery.

Reproduction

Our sample contained no immature males and only 23 immature female vermilion snapper. Testes either contained tailed sperm, suggesting the potential for spawning, or contained brown bodies, suggesting previous spawning. The smallest male examined was 199 mm TL; therefore males must reach maturity at a smaller size than do females. For females, 80% were sexually mature at age 1, and 100% were sexually mature by age 7. More than 90% of the females were mature at 200 mm TL, and 100% were mature at 325 mm TL.

Vermilion snappers in the eastern GOM spawn from May to September. Ripe females were observed during this time period (with the exception of June) (Fig. 6). These fish contained late-stage vitellogenic oocytes, hydrated oocytes, and postovulatory follicles (Fig. 7). Through the rest of the year, there was a progression from mostly resting ovaries during October to mostly early developing ovaries during December. Ripe males were observed throughout the year; they were most common (>60% of testes) from March to September and in January (Fig. 6). For both sexes, median GSIs were low from October to April (<0.01 for females and <0.005 for males, Fig. 8). In May, GSIs increased dramatically (medians equaled 0.034 for females and 0.020 for males) and then gradually decreased through September.

Vermilion snapper batch fecundities ranged from 5535 to 86,811 oocytes from fish measuring 210–298 mm TL (n=27). The relationship between batch fecundity and length was batch fecundity = $317 \times$ (whole weight) $- 3.1624 \times 10^4$, r^2=0.55.

Discussion

Collections

The vermilion snapper that we sampled from the eastern GOM were smaller than those collected during the 1980s from the western GOM. Most hook-and-line-caught fish that we sampled (88%) were between 201 and 325 mm TL and were smaller than fish collected from the Texas Flower Gardens by Zastrow (1984) and Nelson (1988). The fish they sampled were mostly (75%) between 269 and 474 mm TL and 262 and 517 mm TL, respectively. Gear bias is probably not responsible for the differences in length distributions. As in our study, both Zastrow (1984) and Nelson (1988) examined fish caught principally with hook-and-line gear. Furthermore, Nelson (1988) examined the length distributions of vermilion snapper caught with different hook sizes (Mustad no. 2–no. 4/0) and noted no differences in the size of fish caught.

Other factors, such as depth and movement, probably cannot explain the differences between the size distribution of fish caught in our study and that of fish caught in the western GOM. Nelson (1988) caught most vermilion snapper from depths between 60 and 90 m. We do not know the depth at which the fish we sampled were captured; however, the mean depth at which vermilion snapper were caught by the eastern GOM commercial fishery in 1995 was 80 m (Schirripa[4]) and is within the depth range given by Nelson (1988). The presence of larger fish in the western GOM could be the result of larger fish moving from the eastern to western GOM. However, this movement seems unlikely because tagging data suggest that vermilion snapper are residents of reefs and do not travel long distances (Beaumariage, 1964; Fable, 1980; Grimes et al., 1982).

Increases in fishing pressure may have reduced the average size of fish caught by the fishery. Schirripa[4] reported that the average size of fish in the GOM commercial fishery dropped from a high of 371 mm TL in 1984 to a low of 320 mm TL in 1993. Over this same time, commercial landings increased from 1.6 million pounds in 1984 to 2.5 million pounds in 1993, and recreational landings increased from 0.2 million fish in 1984 to 1.2 million fish in 1993.

The sex ratio of GOM vermilion snapper is different from the sex ratio reported for snapper from the SAB. In the GOM, female-to-male sex ratios were not significantly different from 1:1 (Zastrow, 1984; Collins[3]; this study), or they significantly favored males (1:1.2; Nelson, 1988). In the SAB, females significantly outnumbered males, and sex ratios ranged from 1.6:1 to 1.7:1 (Grimes and Huntsman, 1980; Cuellar et al., 1997; Zhao and McGovern, 1997). Zhao and McGovern (1997) partitioned sex ratios from the SAB by depth, fish size, sampling year, gear type, and latitude. Of these, only gear type and latitude significantly affected the sex ratio. Females were proportionally more common in trap and hook-and-line collections than in trawl collections. Although Zhao and McGovern (1997) were cautious about attributing decreases in the proportion of females to changes in latitude, 1:1 sex ratios reported in the GOM (Zastrow, 1984; Collins[3]; our study) and from Puerto Rico (Boardman and Weiler, 1979) are consistent with this hypothesis. We did not find any significant differences in sex ratios by season; however, Zastrow (1984) and Nelson (1988) reported an increase in the proportion of males in the summer in the western GOM.

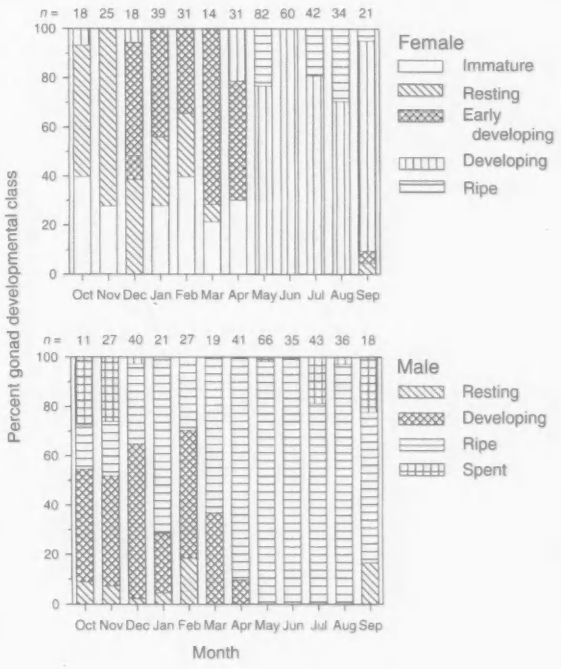

Figure 6

Percentage of vermilion snapper from the eastern Gulf of Mexico in gonad development classes by month and by sex.

Age and growth

Sectioned otoliths can be used to age eastern GOM vermilion snapper and produce higher readability

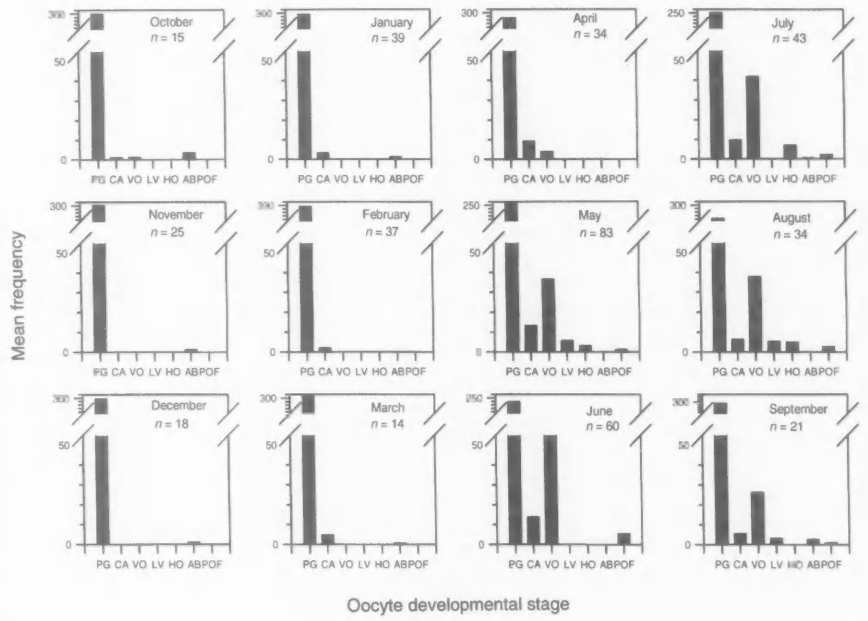

Figure 7

Average frequency of occurrence of oocyte development stages by month for vermilion snapper from the eastern Gulf of Mexico. PG=primary growth oocyte, CA=cortical alveolar oocyte, VO=vitellogenic oocyte, LV=late vitellogenic oocyte, HO=hydrated oocyte, AB=atretic body, and POF=postovulatory follicle.

and agreement rates than scales or whole otoliths can produce. Our readability rates were high (98%) and were similar to rates reported by Zhao et al. (1997), who were able to read 96% of sectioned otoliths from SAB vermilion snapper. The use of whole otoliths has produced mixed results. Barber (1989) had a high agreement rate between readings (84%) and was able to count as many as 26 zones. However, Grimes (1978) found that whole otoliths were difficult to interpret at ages greater than 7. Scales have been used with limited success by Grimes (1978), Zastrow (1984), Nelson (1988), and Collins and Pinckney (1988). Agreement rates between readings in these studies have ranged from 44% to 85% and were lower than reported in this study (100%) and by Zhao et al. (1997) (96%). Grimes (1978) found that counts from scales and whole otoliths from the same fish were similar and reported an agreement rate of 75%.

Marginal-increment analyses suggest that vermilion snapper form one opaque band per year in the late spring and summer. This pattern has also been noted for vermilion snapper captured from the SAB. Zhao et al. (1997) found that opaque zones formed in June for fish age one year and in July for fish ages two to six years. Barber (1989) attempted to use marginal-increment analyses to validate annulus formation in whole otoliths from snapper from the GOM; however, he was unable to show an annual pattern. Grimes (1978) observed that the hyaline layer was formed in November in the SAB. Because hyaline and opaque bands alternate, Grimes's (1978) findings imply that an opaque band is formed once a year before November.

Vermilion snapper are considered long-lived, slow-growing fish (Manooch, 1987). The oldest individual we aged was 13 years old, similar to the SAB maximum age of 12 years reported by Zhao et al. (1997), who also used sectioned otoliths. However, our maximum age was older than the scale-based maximum ages reported for the western GOM of age 7 by Zastrow (1984) and age 10 by Nelson (1988). Those using scales to age fish typically underestimate the ages of older fish (Beamish and McFarlane, 1987). As fish approach their asymptotic size, little or no increase in fish size occurs and this is reflected as little or no increase in scale size. Therefore, rings at the scale edge of older (larger) fish become difficult

to interpret. Barber (1989) reported that otolith-based ages were on average three years greater than scale-based ages for GOM vermilion snapper, although he did not directly compare otoliths and scales from the same fish. Our maximum age was less than the 26 years reported by Barber (1989). His older ages are surprising because he used whole otoliths to estimate age. Grimes (1978) noted that one disadvantage to aging vermilion snapper by using whole otoliths is that rings are difficult to interpret in fish older than age 7. Although we did not compare whole otoliths to sectioned otoliths of vermilion snapper, for gag (*Mycteroperca microlepis*), annuli at the edge of the otolith are more readily observed in sectioned otoliths than in whole otoliths (Collins et al., 1987; Hood and Schlieder, 1992).

Empirical mean lengths and predicted lengths at age were less for our vermilion snapper than for snapper from the western GOM (Table 4; Fig. 9). At age 1, the mean length of fish from our study (211 mm TL) is similar to that of fish from studies by Zastrow (1984; 207 mm TL) and Nelson (1988; 207 mm TL); however, by age 4, the mean length in our study (253 mm TL) is at least 100 mm less than mean lengths in their studies (353 and 357 mm TL , respectively; Fig. 9). If scale-based ages underestimate actual age, then mean length at age and growth rates will be overestimated (Beamish and McFarlane, 1987). However, because scales generally give good estimates of age for younger fish and because the mean length of our fish at age 1 is similar to lengths given by Zastrow (1984) and Nelson (1988), differences in length could reflect differences in growth as opposed to bias from aging structures.

Our estimates of empirical mean lengths and predicted lengths at age, which were lower than those estimates for vermilion snapper from the western GOM, could also be the product of changes in fishing pressure. Schirripa[4] summarized GOM landings data and noted that annual commercial and recreational landings have increased 3- to 4-fold from the mid-1970s to the early 1990s. If larger fish are more vulnerable to capture, then faster-growing fish within an age class will be selectively removed from the population. The result of this type of selection will be a depression of mean size at age for older age classes and an underestimation of the biologically realistic L_∞ (Pitcher and Hart, 1982). This pattern was noted by Zhao et al. (1997) for vermilion snapper in the SAB. Their estimates of growth based on ages from sectioned otoliths for 1979–81 were similar to growth estimates (scale-based ages) by Grimes (1978) from the mid-1970s, when fishing pressure was low. Zhao et al.'s (1997) estimates of size at age and of L_∞ then decreased over time. Estimates of L_∞ dropped from 629 mm TL (1979–81) to 365 (1982–84) and 333 mm TL (1985–93) (Table 4). They could not attribute declines in size at age or L_∞ to gear selectivity, sampling regime, depth, or latitude and concluded their observed changes were due to selective fishing for faster-growing individuals within all age classes.

Similar decreases in observed lengths at age have been reported for red porgy, a species often found in the same habitats as vermilion snapper (Grimes et al., 1982; Barans and Henry, 1984; Chester et al., 1984; Sedberry and Van Dolah, 1984; Nelson, 1988) and sought by the same fisheries (Grimes et al, 1982; Nelson, 1988; Collins and Sedberry, 1991). Average total length of GOM red porgy reported by Hood and Johnson[7] at age 6 years was 348 mm and was over

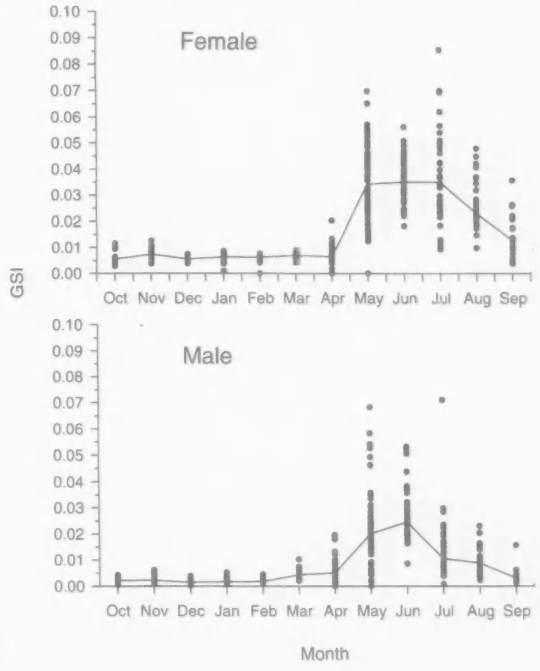

Figure 8

Monthly gonosomatic indices (GSI) for female and male vermilion snapper from the eastern Gulf of Mexico. Median values are connected by the solid line.

[7] Hood, P. B., and A. K. Johnson. 1997. Age, growth, mortality, and reproduction of red porgy (*Pagrus pagrus*) from the eastern Gulf of Mexico. Florida Marine Research Institute, Florida Department of Environmental Protection, 100 Eighth Avenue S.E., St. Petersburg, Florida. Manuscript in prep.

100 mm less than the average length of 464 mm reported by Nelson (1988). In the SAB, the average total length of 6-year-old fish had decreased from 451 mm in 1972–74 (Manooch and Huntsman, 1977) to 363 mm in 1991–94 (Harris and McGovern, 1997). Both Harris and McGovern (1997) and Hood and Johnson[7] concluded that the observed decrease in average length at age was likely due to size selective fishing.

Mortality

The age of full recruitment to both the recreational and commercial fisheries has increased since the early 1980s. Zastrow (1984) and Nelson (1988) reported the age at full recruitment to be 4 years, less than our estimate of 6 years. The reported age of full recruitment to the SAB hook-and-line fishery was 4 years before 1981 (Grimes, 1978; Huntsman et al., 1983; Zhao et al., 1997) but increased to 6 years by 1993 (Cuellar et al., 1996; Zhao et al., 1997). This increase in age of recruitment has been associated with a decrease in length at age attributed to selective fishing on faster-growing members of each age group (Zhao et al., 1997). Our estimates of mortality (0.469–0.489) are within the range given by Schirripa[4] for the years 1986–1995 in the GOM (0.466–0.791) and less than the estimate from the SAB headboat fishery (0.67) reported by Huntsman et al. (1983).

Reproduction

Our observed sizes of maturation were less than those reported by Nelson (1988) for the western GOM. We found that most females were sexually mature at 200 mm TL (age 1), and we did not examine any immature males (the smallest male we sampled was 199 mm TL). The smallest mature female and male reported by Nelson (1988) were 234 mm TL and 291 mm TL, respectively. In the SAB, Collins and Pinckney (1988) found that at 160 mm TL, 60% of females and 90% of males were mature. Cuellar et al. (1996) sampled females as small as 186 mm TL and males as small as 197 mm TL and did not find any immature fish in their samples. These lengths at maturity are in contrast to the results of Grimes and Huntsman (1980) who found that SAB vermilion snapper matured between 186 and 324 mm TL (ages 3 and 4). There is an indication that increasing fishing pressure may depress vermilion snapper size and age at maturity. Zhao and McGovern (1997) noted a decrease in the size at maturity for males and females in the SAB from 1970 to 1992. Before 1982, 31% of males and 5% of females were mature at 140 mm TL. After 1982, all males and 37% of females were mature at 140 mm TL. They suggested that this change may have been caused by the increasing and selective fishing pressure that occurred during the 1980s.

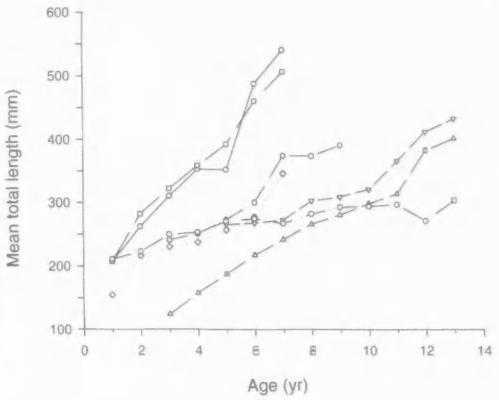

Figure 9

Mean empirical total length at age for vermilion snapper from the eastern and western Gulf of Mexico. Scale-based ages from the western Gulf of Mexico by Zastrow (1984; circle, solid line) and Nelson (1988; square). Scale-based ages from Barber (1989) from the eastern (diamond) and western (hexagon) Gulf of Mexico. Whole-otolith-based ages from Barber (1989) from the eastern (triangle) and western (inverted triangle) Gulf of Mexico. Sectioned-otolith-based ages from this study (circle, dashed line).

On the basis of the presence of ripe females and increases in GSI, we believe that vermilion snapper in the GOM spawn from May to September. Nelson (1988) and Collins[5] also reported summer spawning. In our samples, ripe gonads were present from late spring to early fall but were most common from May to July. In addition, GSIs were highest during the summer months. Spawning seasonality in the GOM is similar to that reported for the SAB, where fish spawn from the late spring to early fall (Grimes and Huntsman, 1980; Cuellar et al., 1996). Boardman and Weiler (1979) found that in Puerto Rican waters, spawning takes place year round.

Batch fecundity was positively correlated with fish length. Nelson (1988) and Collins[5] also found a positive relationship between batch fecundity and length for GOM fish. Their estimates were larger than those obtained in our study (61,600–392,000 and 33,550–415,161 oocytes, respectively); however, the fish sampled were also larger (209–510 and 248–375 mm TL, respectively). Our estimates of batch fecundity were similar to SAB estimates reported by Cuellar

Table 4

Von Bertalanffy growth parameters for vermilion snapper from the Gulf of Mexico (GOM) and South Atlantic Bight (SAB). Table adapted from Goodyear and Schirripa.[3] Our study and the studies of Schirripa[4] and Zhao et al. (1997) were added to the table. L_∞ is the asymptotic TL, K is the von Bertalanffy growth coefficient, t_0 is the time that TL is zero, and n is the sample size.

Study and area	Aging structure	Sex	n	L_∞ (mm)	K	t_0
Current study						
Eastern GOM	otoliths	Combined	841	298	0.25	–3.9
Schirripa[1]						
GOM	scales and otoliths	Combined	586	535	.203	–0.94
Nelson (1988)						
Flower Gardens, TX	scales	Combined	906	554	0.22	–0.30
Barber (1989)						
St. Petersburg, FL	scales	Combined	34	936	0.05	–3.37
Pensacola, FL		Combined	194	344	0.16	–3.356
Galveston, TX		Combined	799	561	0.10	–2.81
Port Aransas, TX		Combined	270	428	0.15	–2.78
Brownsville, TX		Combined	779	477	0.16	–2.32
St. Petersburg, FL	otoliths	Combined	1113	469	0.09	–1.16
Pensacola, FL		Combined	600	511	0.08	–1.44
Galveston, TX		Combined	799	554	0.08	–1.46
Port Aransas, TX		Combined	270	657	0.07	–1.18
Brownsville, TX		Combined	779	603	0.09	–0.87
Grimes (1978)						
SAB	scales	Combined	815	627	0.20	–0.13
Zhao et al. (1997)						
1979–81	otoliths	Combined	195	629	0.202	–0.117
SAB 1982–84		Combined	265	365	0.315	–0.361
1985–93		Combined	766	333	0.271	–0.899

[1] Schirripa, M. J. 1992. Analysis of age and growth of vermilion snapper with an assessment of the fishery in the Gulf of Mexico. National Marine Fisheries Service, Southeast Fisheries Center, Miami Laboratory, Miami, FL. CRD-91/92-

et al. (1996; 4000 to 90,000 oocytes from fish 186–340 mm TL).

Summary

Recent stock assessments of vermilion snapper suggest that vermilion snapper stocks in the GOM are overfished (Schirripa[4]). Our study, when compared to previous studies of vermilion snapper, suggests that size-selective mortality coupled with overfishing may be responsible for changes in life history parameters (decreases in the mean length at age, estimated L_∞, and length and age of maturation). If these changes are not taken into consideration, estimates of the yield-per-recruit, mortality, and spawning potential ratios that use the above life history parameters in their calculations could be biased. Consequently, erroneous conclusions about the health of the stock of GOM vermilion snapper could be made in future stock assessments.

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Movement of Atlantic cod, *Gadus morhua*, tagged in the Gulf of Maine area

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Abstract.—Over 22,000 Atlantic cod, *Gadus morhua*, were tagged with T-bar tags and released in the Gulf of Maine area in 1984–97 and 2400 recovered tags were used to interpret movement of tagged fish. Most of the releases were of adult fish made during the winter cod spawning season from aggregations found on known spawning banks. Recaptures by NAFO divisions were weighted with an annual index of fishing effort to account for probability of recapture. At the division level, very little exchange between the area east of 4X and the Gulf of Maine was evident. However, within the Gulf of Maine an exchange of about 15% between 4X and 5Z and somewhat higher between 4X and 5Y was apparent. Cod tagged on Browns Bank and Georges Bank during the spawning season showed widespread dispersal both within their respective division and to adjacent divisions. The seasonal distribution of recaptures in 4X indicates aggregation for spawning followed by postspawning dispersal. The seasonal pattern for Georges Bank is less clear but there are indications of net loss to the 4X area. Distribution of recaptures from Georges Bank releases in 1994 was similar to those observed for releases made in 1984–85. Results of the study were consistent with results from earlier tagging experiments and demonstrate substantial interaction of cod from different management areas. These findings may have implications for stock assessment models and management objectives.

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Fish. Bull. 97:842–860 (1999).

The Atlantic cod (*Gadus morhua*) is a demersal species with a wide Northwest Atlantic geographic range extending from the Gulf of Maine in the south to the Davis Strait in the north (Scott and Scott, 1988). It is one of the most important commercially exploited groundfish species in Atlantic waters off Canada and the eastern U.S. region, and cod stocks have supported fisheries in the Gulf of Maine since the 1700s (Serchuk and Wigley, 1992).

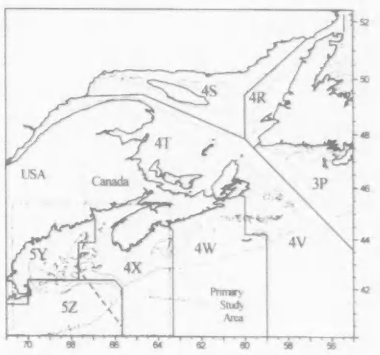
The Gulf of Maine area, as defined in this study, includes waters of the Bay of Fundy, Georges Bank to 71°41'W, and the Scotian Shelf west of 63°20'W, an area of approximately 150,000 km^2. There are four fisheries management units identified for Atlantic cod in this area, based on known areas of spawning aggregation and commercial fisheries (Halliday et al., 1986). Geographic boundaries of North Atlantic Fisheries Organisation (NAFO) divisions and the U.S. National Marine Fisheries Service (NMFS) and Canadian Department of Fisheries and Oceans (DFO) unit areas (Fig. 1) are used to approximate the distribution of the stocks. The present management units are division 4X, subdivision 5Ze in unit areas j and m (Canada), subdivision 5Zw+SA6 (USA) and division 5Y. The area is also divided by the International Maritime Boundary (IMB) between Canada and the United States, established in 1984. Halliday and Pinhorn (1990) have provided an extensive review of the basis for existing statistical areas used to report fisheries activities and note that unit areas were established in the early 1970s.

Population characteristics of the four cod stocks have been reported by Canada (Clark 1996; Hunt and Buzeta 1996) and by the United States (NEFSC, 1994). Stock abundance has shown substantial variation in the last fifteen years and a broad range of recruitment. In general, all the stocks have declined from the long-term average abundance and, with the exception of the 4X stock, appear to be at low levels of spawning stock biomass.

Numerous tagging studies have been undertaken to examine movement of cod in the Gulf of Maine area. Hunt and Neilson (1993) provided a synopsis of tag-recapture

results from experiments conducted between 1923 and 1960. An earlier summary of cod tagging studies is given in Wise (1963). Templeman (1962) provided a comprehensive summary of the basis for separating cod stocks in the northwest Atlantic using meristic and results of tagging experiments and concluded "there are Browns Bank and eastern Georges Bank stocks, probably essentially separate as spawning stocks but with some intermigration in both directions across the Fundian Channel and some intermingling of both these stocks with those of southwestern Nova Scotia." In general, results of these early experiments indicate substantial movement of cod within the 4X area and to a lesser extent to and from the adjacent 5Y and 5Ze areas. The pattern of recapture locations shows a general dispersal from the area of release and some increase in the number of cod moving with elapsed time. However, it is difficult to interpret these studies as proportional movements because landings and effort are generally not available for weighting probability of recapture by area.

Canada has conducted a number of tagging studies on cod in the Browns Bank, Georges Bank, and Bay of Fundy areas since the 1970s. Studies conducted between 1994 and 1996 were part of a co-operative research study involving Canada and the United States. This report provides an interpretation of cod movements in the Gulf of Maine area based on results of recaptures of cod tagged in the 1979–97 time period.



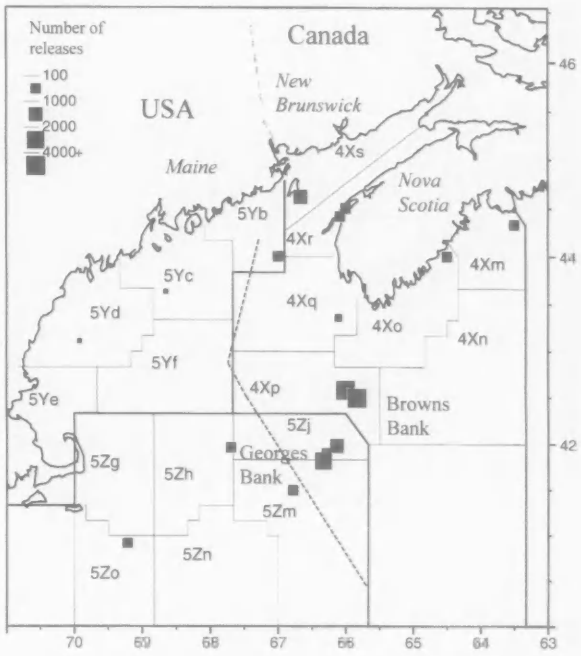


Figure 1

North Atlantic Fisheries Organization (NAFO) division (4X, 5Y, 5Z) and unit areas (eg. 5Zj) boundaries in the Gulf of Maine area and cod tag release locations. The dashed lines indicates the International Maritime Boundary line between Canada and the United States.

Methods

Canada has conducted stratified random bottom trawl surveys in the Gulf of Maine since 1970 and on Georges Bank since 1986. The United States has also conducted similar surveys in the spring (1968) and fall (1963) of each year. Indices of abundance derived from these surveys are routinely used in stock assessment models to estimate population abundance (Hunt and Buzeta, 1996), and they provide a synoptic view of cod distributions in the Gulf of Maine area during both spawning and postspawning seasons. The mean catch per tow, aggregated by ten-min latitude and longitude squares, was calculated for the U.S. spring and fall research-vessel time series. These surveys cover most of the Gulf of Maine area, compared with the Canadian summer survey (4X only) and Canadian winter survey (5Ze only), and therefore provide a distribution pattern for cod in the entire study area.

Tagging locations were determined from areas of high catch rates in research vessel surveys, as well as the location and timing of historical cod spawning activity. Additional tagging was completed during other times in areas of fishing activity or special interest locations. Fishing trials were used to identify sites with high catch rates and at least 50% cod composition, and new sites were selected when catch rates or cod composition declined. Typically, once an aggregation of cod was located, fishing and tagging continued at that site for 1–2 days. Areas with high

catches of skates (*Raja* spp.) and dogfish (*Squalus acanthias*) were avoided because their abrasive skin resulted in damage to cod and poor quality specimens for tagging.

Fisheries research stern trawlers, 50–70 m in length, equipped with a research Western IIa otter trawl and with wet laboratory facilities below the trawl deck, were used for large-scale tagging operations. Fishing operations consisted of 5–20 min tows at depths ranging from 40 to 70 fathoms. At the end of each tow, cod were released into a sluice way leading to the below-deck wet laboratory area and transferred into 1500-L holding tanks with recirculating ambient sea water. Viability of each cod was assessed prior to tagging and fish in poor condition or that had apparent external injuries were discarded. Control experiments to assess tag or stress induced mortality were not conducted, but observation showed that even fish that were initially inverted or dormant on the bottom of the tank returned to an apparent active and normal behavior within 15–30 minutes. Tagged fish were released through a sluice way exiting about one to two meters above the water line. Approximately 100 to 250 cod could be held, tagged, and released from each tow, depending on average fish size in a tow.

Fish to be tagged were removed from holding tanks by hand with dip nets and placed on a measuring board to obtain length. A tag was inserted near the leading edge of the first dorsal fin and the fish was released. Total elapsed time from start to end of the tagging operation was in most cases less than 30 seconds for each fish. An *ad hoc* representative sample was examined to verify the spawning state of reproductive development (Hunt, 1996) but results were not recorded.

Several small-scale cooperative studies were carried out with commercial fishing vessels. The first of these opportunistic tagging operations was conducted aboard the U.S. FV *Mary V*, a longline vessel fishing out of Gloucester, MA. During routine fishing operations on the northern edge of Georges Bank, cod caught that were less than the U.S. minimum legal size (49 cm 19 inches) were tagged by the vessel's crew and released. Tags were also supplied to staff of the Massachusetts Division of Marine Fisheries (MA-DMF) and the Maine Department of Marine Resources (ME-DMR) to use during trips when onboard fishery observers were present on commercial longliners fishing in the Nantucket Shoals (MA-DMF) and on commercial charter boats fishing the inshore waters of the Gulf of Maine (ME-DMR). During these trips, undersize cod were also tagged and released. A small number of cod, taken as bycatch in lobster traps during the winter lobster fishing season (4Xq inshore), were tagged and released by Canadian fishermen.

All tags were of the T-bar type (FD-67 and FD-94 in 1994) applied with the Mark-II tag insertion gun and were supplied by Floy Tag and Manufacturing, Inc (4616 Union Bay Place NE, Seattle, WA 98105). Overall length of the tag was about 6.5 cm and each tag had a 3.5-cm bright yellow address sleeve and a 1.0-cm attachment T-bar. Each tag was imprinted with a unique identification number and Canadian return mail address on the vinyl sleeve. Tags used in the 1994 experiment included a second mailing address for the National Marine Fisheries Service (NMFS), Northeast Fisheries Science Center, Woods Hole, MA. Tags were provided in clips of fifty with consecutive numbering to facilitate record keeping.

An extensive advertising campaign, targeting Canadian and U.S. fishing enterprises and communities, was completed prior to and after each of the large-scale tagging experiments. This included notices in local newspapers and other industry publications, all-weather bilingual posters located at major fish landing and processing facilities, personal contact with industry representatives, and follow-up with individuals submitting tags. A representative of the fishing sector participated in the 1994 experiment to obtain firsthand knowledge of operations and, as was hoped, to convey the importance of returning tags to colleagues.

In Canada, a nominal reward of seven dollars was offered for each tag returned. In the United States, a reward of five dollars was paid for tags returned with recapture information and two dollars for tag only returns. In addition to the reward, the finder was provided with a summary of release and recapture information for each tag returned.

All release and recapture data were loaded to a database to facilitate analysis. Tag-recapture information was edited to eliminate obvious errors such as onshore recoveries, substantial decreases in fish length, unrealistic travel and elapsed time factors, etc. Quality of recapture data was variable, ranging from no information to a detailed record of how, when, and where (latitude and longitude) fish were caught, fish size at recapture, age determination material, and other anecdotal information. About 80% of recaptures included detailed information on location and about 20% had length-at-recapture measurements.

Analysis of recapture data was completed first at the divisional level, then at the unit area level for the Gulf of Maine and finally at 10-min latitude and longitude squares. Results were compiled to show movement from area of release to adjacent areas and, conversely, movement to an area from adjacent sites. Analysis of recapture patterns at the divisional level

was used to assess exchange between management areas. Observed numbers of returns were used for this purpose because exploitation rates and commercial fishery landings, required for weighting, were not as readily available for areas outside of the Gulf of Maine area. All releases and recaptures in divisions 4W, 4V, 4T, 4R, 4S, and subarea 3, which were geographically east of the division 4X-4W boundary, were grouped for this part of the analysis; we refer to this combined geographic area as "east of 4X."

Because recaptures from tagging studies are usually dependent on commercial fisheries, the distribution and abundance of recaptures is a function of the distribution of fishing effort as well as of fish movements. In an attempt to account for the effect of fishing effort, we weighted recaptures using the commercial fishery exploitation rates for cod stocks in the area. Landings, effort, and exploitation rates of cod by unit area were obtained from the published literature (NEFSC, 1994; Clark, 1996; Hunt and Buzeta, 1996). No provision was made for potential discarding, misreporting of catches, or allocation to unit area. The extent of these problems in landing statistics are thought to be substantial in some years and areas but have not been quantified (Clark, 1996; Hunt and Buzeta, 1996). A review of both the quality and quantity of effort data indicated that a low proportion of landings, particularly for fixed gear components, were represented. Therefore, direct measures of effort could not be used to make adjustments to returns on the basis of distribution of effort. However, trends in landings by unit area and fleet composition showed a relatively stable spatial and seasonal pattern. In some years a considerable proportion of total Canadian landings from division 4X was not allocated to a specific unit area. On the basis of preliminary work by Clark (1996), an algorithm was applied to allocate this unspecified proportion to unit area. The reported annual exploitation rate for each stock was then partitioned according to annual percent of unit area landings and used as a year- and area-specific index of the probability of recapture:

$$A_{a,y} = \Sigma C_y / (C_{a,y} \times E_y),$$

where A = adjustment factor;
C = percent of annual reported landings by management area;
E = reported annual exploitation rate by management area;
$_a$ = unit area; and
$_y$ = year.

Within a year, tag recaptures from areas with low landings were therefore given higher relative weighting than those from areas of high landings. Annual differences in exploitation rate were used to weight for between-year effects. The derived adjustment factors were standardized to the unit area and year with the lowest landings and exploitation rate.

Summaries of tag recaptures within an area by area of release required standardisation to reduce the impact of large numbers of releases from some areas. For example, the large number of releases from the Browns Bank area and subsequent number of recaptures would tend to overshadow recaptures from small-scale releases. Therefore all recaptures for this part of the analysis were standardized to the equivalent number of recaptures from 1000 releases.

Seasonal effects of cod movements were evaluated for the two Browns Bank and Georges Bank release sites. Recaptures from these sites were aggregated by quarter with recaptures in the first month after release excluded. Results were summarized by unit area within the release division.

To evaluate temporal effects, data were partitioned into groups representing recaptures from 0–12 months, >12 months after release, and total recaptures. The influence of size at release was also investigated but initial examination showed no substantial difference in either direction or distance among size groups. This may be due to the fact that most fish were greater than the L_{50} mature reported by Hunt (1996) for Georges Bank cod at the time of release and would be expected to diminish the potential impact of size on movement.

Recapture information that included latitude and longitude was used to summarize the tag recoveries by 10-min latitude and longitude squares for the Browns and Georges Bank release sites. Recaptures in each square were weighted by the adjustment factor index associated with the unit area in which the square was located. The Browns Bank and Georges Bank areas support substantial commercial fisheries and are thought to be centers of spawning activity. Tag releases were made during the spawning season and therefore recoveries should represent movement of postspawning fish.

The minimum, maximum, and average time at large after tagging was calculated for releases from each unit area. For recaptures with latitude and longitude location, the straight line distance between release and recapture site was calculated to determine the minimum, maximum. and average distance travelled.

A small proportion of recaptures included size at the time of recapture and these were used to estimate individual specific growth rates. The increase in length between release and recapture was adjusted to an annual value ((increment × 365)/days at large)

for each fish and averaged by 10-cm intervals of release length to give an annual growth rate.

Results

Average cod catches per tow, derived from U.S. spring and fall research surveys for 1982–91, are shown in Figure 2, A and B, and indicate widespread distribution throughout the area with some apparent centers of aggregation associated with banks. Densities and distributions show seasonal variation between the spring and fall. In the spring, distribution (with localized areas of high density) appears to be contiguous from Cape Cod, across Georges Bank, to Browns Bank and then farther east and west to the Bay of Fundy. In the fall, densities are lower and there is more apparent geographic isolation. Gavaris et al. (1993) found similar results when comparing seasonal distributions in relation to the IMB line in the Georges Bank area. The central part of the Gulf of Maine area has relatively low densities for both spring and fall seasons.

Over 58,000 releases were included in our study of which about 22,300 were in the Gulf of Maine primary study area. The release sites in the Gulf of Maine area, aggregated by ten-min latitude and longitude squares, are shown in Figure 1 and summarized by date and unit area in Table 1. Releases by area ranged from about 11,000 in 4Xp (Browns Bank) to only seven in 5Yd. Total recaptures were more than 6300 with over 2400 from the Gulf of Maine. Return rate by area varied between 0% and 34% with an average of 9%. Release length ranged from about 15 cm to about 140 cm. A relatively high proportion of released fish were >80 cm in the 5Zj area. The majority of released cod were larger than the L_{50} maturity (~43 cm; see Hunt 1996), with the exception of unit areas 4Xm and 4Xo.

Observed numbers of recaptures by division of release and recapture for each of "east of 4X," 4X, 5Y, and 5Z areas are shown in Figure 3. Over 97% of cod recaptured from releases east of 4X were also recovered east of 4X and, conversely, 74% of fish recaptured in this area originated from releases east of 4X. Further analysis of information on the area east of 4X is required but, in general, movement between this area and the Gulf of Maine appears to be limited. For division 4X, 80% of recaptures from releases in 4X occurred in 4X, with 8% moving east of 4X and 12% west to 5Z and 5Y. Of the total recaptures taken in 4X, 50% were from 4X releases, 42% from 5Y releases, and 8% from division 5Z releases. In division 5Y, 63% of recaptures from releases in 5Y occurred in 4X and of these only 21% occurred in 5Y and 2% from 5Z. However, of the total recaptures in 5Y, over 80% were from 5Y releases and 17% from 4X. The high proportion of recaptures in 5Y from division 4X is probably influenced by the small numbers of releases and recaptures as well as the distribution of commercial fishing in the vicinity of the 4X and 5Y boundary. Clark (1996) noted that Canadian land-

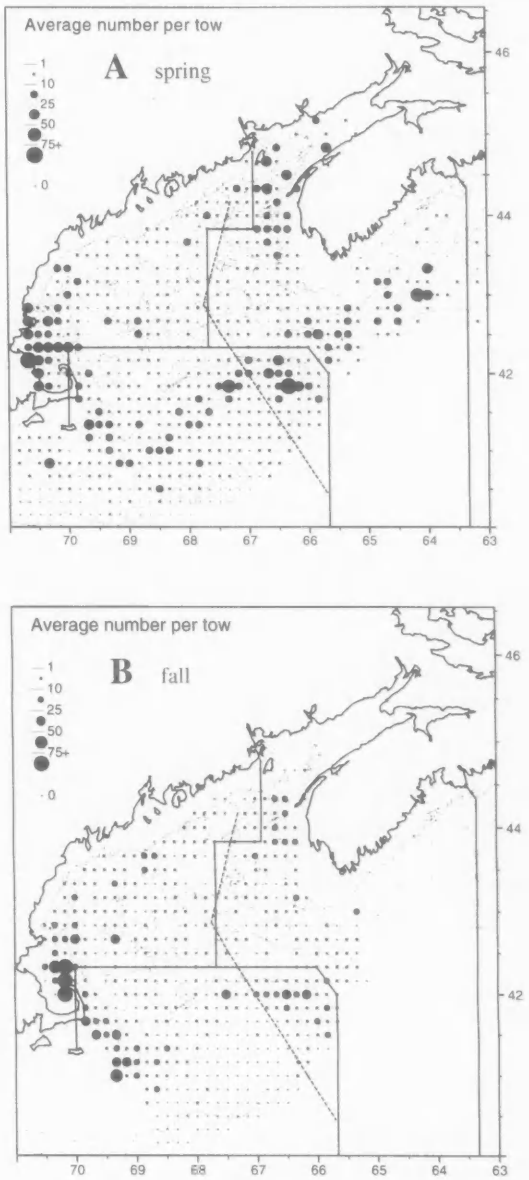


Figure 2

Mean catch per tow of cod derived from 1982–91 U.S. research surveys in the Gulf of Maine area: (**A**) spring and (**B**) fall.

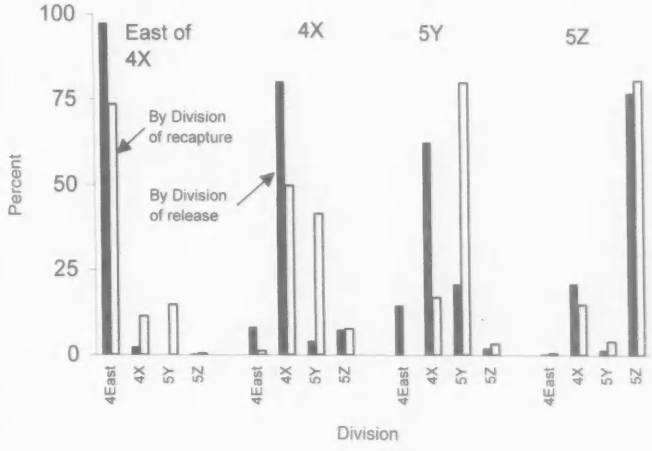


Figure 3

Percent of cod tag recoveries by NAFO Division of release (solid bar) and Division of recapture (pattern bar, based on 1000 releases) for divisions 4X, 5Y, 5Z, and the area east of 4X.

ings from the 5Y area near the 4X-5Y boundary are considered part of the 4X fishery and therefore were included in our 4X stock assessment. In division 5Z, 77% of cod released in 5Z were recaptured in 5Z and 21% were recaptured in 4X. Of the total recaptures in division 5Z, 81% were from 5Z releases and most of the movement out of the area occurred to the northeast (15%), towards division 4X.

The annual percent exploitation rate of cod by management area (4X, 5Y, 5Z) is summarized in Figure 4 for the 1980–97 time period. Reported landings by unit area showed considerable variation but proportions were relatively stable over time. In division 4X, unit area 4Xo accounted for about 38% of the 1980–97 total landings and unit area 5Yd for about 40% of the 5Y total. In subdivision 5Ze, unit areas 5Zg (30%) and 5Zj (40%) dominated, representing the U.S. and Canadian fisheries, respectively. The derived recapture adjustment factors, standardized to a maximum of 1.00, are given in Table 2 for each year and unit area. Annual factors ranged from 0.02 to 1.00, meaning that about 100 recaptures from a unit area with high landings and exploitation were proportionally equivalent to about two recaptures from a unit area with low landings and exploitation rate.

The effect of weighting tag recoveries to account for fishing effort is shown in Figure 5 for releases in the Browns Bank area. Weighted recoveries decrease the apparent extent of movement to 4Xo and 5Zj, because of their relatively high landings and exploitation rates, and increases the contribution of 4Xp recoveries. Similar effects are seen for other unit areas.

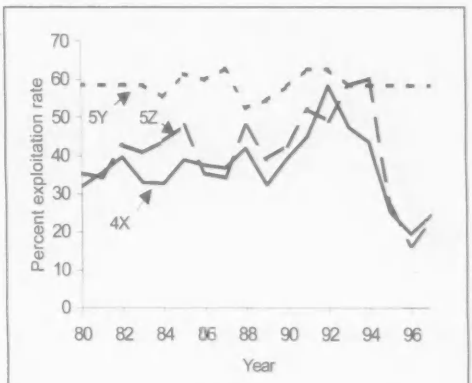


Figure 4

Reported percent exploitation rate of cod by the commercial fishery in management areas 4X, 5Y, and 5Z for 1980–97.

Table 3 provides a detailed summary of recaptures by unit area of release and recapture partitioned into <12 months elapsed time from release and the total number of recaptures. The observed number of tag returns, the number adjusted by unit area landings, and the percent of total adjusted number are shown. The percent of recaptures reported is based on only those released and recaptured in the Gulf of Maine

area. Table 3 summarizes results by area of release and shows the pattern of movement away from the release site (or no movement when the area of release=area recapture). Table 3 shows the pattern of movement into an area from standardized releases in adjacent areas and is organized so that the two aspects of tag recoveries appear on the same horizontal line. For example, in the second row of data, results show 31.4% of cod released in 4Xm were recaptured in 4Xo, whereas only 15.5% of cod recaptured in 4Xm originated from 4Xo releases.

About 63% of the cod tagged in 4Xm appeared to remain in the area although there was some movement to the west into adjacent areas. Over 76% of cod recaptured in 4Xm originated from 4Xm releases. At the divisional level, movement in relation to the division 4X/4W boundary is small (Fig. 3); however, exchange between divisions does occur and is concentrated in the 4Xm, 4Xn, and 4Xo areas.

No releases were made in 4Xn but about 80 recaptures were taken in the area. Most of these recaptures were from the Browns Bank (46%) and Georges Bank (27%) releases. Additional recaptures originated in the Bay of Fundy area and about 4% from the area east of 4X.

Results for the 4Xo area indicate a contrast between the two analyses of recaptures. Close to 100% of recaptures of cod released in the 4Xo area were

Table 1

Summary of cod tag releases and recaptures in NAFO divisions by release date. * indicates release from commercial fishing vessels.

Area released	East of 4X	4Xm	4Xo	4Xp	4Xq	4Xr	4Xs	5Yb	5Yc	5Yd	5Zj	5Zm	5Zo
Date	1978–81	Feb 80	May 79	Feb 84	Dec 94*	Jun 79	Aug 84	Jul 85	Jun 94*	Jul 94*	Feb 84	Mar 94	Jul 94*
N	36,338	808	694	3,980	50	141	67	350	27	7	1988	843	100
Length range (cm)	15–135	13–92	21–87	33–140	36–64	22–75	38–100	33–112	34–47	36–43	16–136	31–130	35–48
Mean length (cm)	48.8	47.9	41.9	71.9	47.4	36.7	57.1	59.9	41.1	40.3	61.2	69.9	42.4
Date				Mar 84	May 94*	Jul 85	Dec 85				Mar 85	Jun 94*	
N				786	4	216	73				500	266	
Length range				40–126	38–57	28–103	26–64				33–139	30–50	
Mean length				66.3	43.5	52.9	42				72.1	44.4	
Date				Feb 85	Dec 95*		Jul 85				Mar 94		
N				1,621	9		1399				3608		
Length range				38–142	38–72		26–94				30–144		
Mean length				79.8	48.1		52.6				73.8		
Date				Mar 85	May 96*		Nov 85						
N				4363	58		281						
Length range				32–140	39–85		28–87						
Mean length				72.9	58.8		48.9						
Date					Nov 96*		Jan 85						
N					17		4						
Length range					39–72		36–56						
Mean length					53.8		42.3						
Date							Jul 94*						
N							21						
Length range							36–47						
Mean length							40.3						
Total released	36,338	808	694	10,750	138	357	1845	350	27	7	6096	1109	100
Total recaptures	3883	100	237	1346	1	57	139	49	0	0	476	29	0
Percent recaptures	10.7	12.4	34.1	12.5	0.7	16.0	7.5	14.0	0.0	0.0	7.8	2.6	0.0

recaptured in 4Xo. Cod tagged in 4Xo were from an inshore area and may have been part of a local resident population. About 90% of tags recovered in 4Xo were from fish released in 4Xo and additional small contributions were from other Gulf of Maine locations.

The largest number of releases was from the Browns Bank area and results indicate a widespread dispersal within the Gulf of Maine. The majority of recaptures were from division 4X; substantial numbers of cod moved to the inner Bay of Fundy and smaller numbers moved east to 4Xn and 4Xo. About 33% of cod released in 4Xp were recaptured in the same area. Movement into Divisions 5Y and 5Z accounted for about 15% of the total releases. Of cod recaptured in 4Xp, about 50% originated from the same area, 27% from 5Yb, and about 11% originated from the Georges Bank area. Differences between immigration and emigration distributions may be due to seasonal patterns and commercial fishing operations. The Browns Bank area has been closed to commercial fishing during the winter spawning season and there is a low probability of capture during this time. Cod recaptured during the summer–fall fishing season may represent postspawning dispersal patterns.

In 4Xq, all three of the recaptures were taken in 4Xo. However, cod caught in 4Xq appeared to originate from diverse locations including 39% from 5Yb, 28% from Browns Bank, 20% from the inner Bay of Fundy, and 10% from Georges Bank.

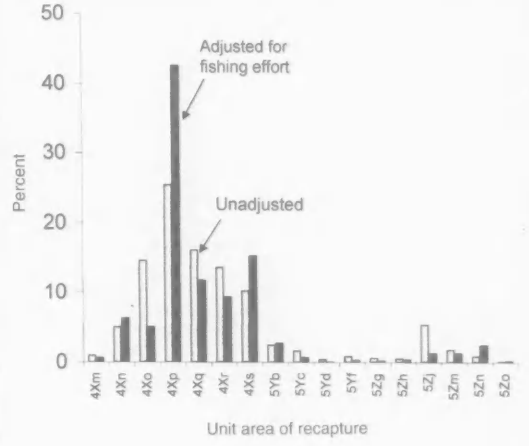


Figure 5

Comparison of percent recaptures by unit areas for Browns Bank releases using observed and effort-adjusted tag recoveries.

Unit area 4Xs and 4Xr represent the inner Bay of Fundy region. Movement of cod appears to occur into and out of the region as well as across the Bay from the Nova Scotia to New Brunswick sides. Over 75% of recaptured cod released in these areas were re-

Table 2

Annual adjustment factors by year and area used to prorate recoveries for probability of recapture, standardized to 1.00 for the area and year (5Zn, 1987) with the lowest landings and exploitation rate.

Area	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	Mean
4Xm	0.13	0.13	0.10	0.16	0.20	0.10	0.10	0.10	0.13	0.24	0.17	0.14	0.14	0.14	0.19	0.71	0.84	0.67	0.24
4Xn	0.21	0.28	0.18	0.32	0.20	0.25	0.17	0.17	0.18	0.32	0.41	0.22	0.12	0.12	0.28	0.30	0.47	0.36	0.25
4Xo	0.07	0.05	0.05	0.06	0.07	0.06	0.06	0.06	0.04	0.06	0.04	0.04	0.02	0.04	0.04	0.12	0.14	0.14	0.06
4Xp	0.44	0.33	0.25	0.22	0.27	0.29	0.54	0.24	0.15	0.12	0.18	0.14	0.15	0.14	0.14	0.13	0.25	0.23	0.23
4Xq	0.19	0.24	0.14	0.16	0.15	0.12	0.11	0.12	0.12	0.17	0.12	0.13	0.08	0.10	0.11	0.16	0.24	0.17	0.15
4Xr	0.15	0.12	0.11	0.13	0.12	0.11	0.13	0.23	0.21	0.24	0.16	0.09	0.07	0.08	0.10	0.21	0.24	0.14	0.15
4Xs	0.30	0.30	0.27	0.34	0.36	0.23	0.23	0.28	0.28	0.46	0.23	0.15	0.16	0.15	0.21	0.50	0.43	0.28	0.29
5Zg	0.04	0.05	0.04	0.05	0.05	0.04	0.07	0.08	0.05	0.05	0.05	0.04	0.06	0.04	0.03	0.06	0.11	0.08	0.06
5Zh	0.14	0.16	0.16	0.12	0.13	0.12	0.25	0.16	0.10	0.15	0.20	0.13	0.14	0.08	0.08	0.17	0.33	0.24	0.16
5Zj	0.08	0.06	0.04	0.04	0.05	0.04	0.05	0.04	0.03	0.05	0.04	0.03	0.02	0.02	0.03	0.20	0.23	0.12	0.06
5Zm	0.33	0.26	0.23	0.23	0.10	0.10	0.13	0.22	0.10	0.13	0.15	0.11	0.12	0.08	0.11	0.32	0.55	0.62	0.22
5Zn	0.39	0.40	0.71	0.97	0.28	0.38	0.79	1.00	0.57	0.53	0.32	0.21	0.34	0.19	0.15	0.33	0.64	0.46	0.48
5Zo	0.49	0.76	0.44	0.38	0.29	0.22	0.32	0.78	0.34	0.40	0.32	0.27	0.46	0.33	0.18	0.41	0.79	0.57	0.43
5Yb	0.61	0.76	0.41	0.31	0.30	0.15	0.19	0.13	0.33	0.44	0.28	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.24
5Yc	0.15	0.15	0.10	0.11	0.10	0.08	0.06	0.06	0.13	0.07	0.07	0.08	0.08	0.09	0.09	0.09	0.09	0.09	0.09
5Yd	0.02	0.02	0.03	0.03	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
5Ye	0.02	0.02	0.02	0.02	0.03	0.03	0.04	0.05	0.04	0.05	0.05	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
5Yf	0.12	0.09	0.07	0.09	0.08	0.05	0.06	0.05	0.12	0.09	0.07	0.07	0.07	0.08	0.08	0.08	0.08	0.08	0.08

Table 3

Summary of cod tag recaptures ordered by area of release and area of recapture (per thousand).

Release area	Recapture area	<12 months total			Total			Recapture area	Release area	<12 months total			Total		
		Number recaptured	Adjusted number	Percent	Number recaptured	Adjusted number	Percent			Number recaptured	Adjusted number	Percent	Recapture recaptured	Release number	Percent
4Xm	4Xm	14	52	55.4	25	92	63.4	4Xm	4Xm	17.2	69.0	73.1	30.7	120.7	76.9
	4Xo	4	37	39.2	5	46	31.4		4Xo	4.3	18.5	19.7	5.7	24.4	15.5
	4Xp	1	2	2.5	2	5	3.2		4Xp	0.6	2.4	2.5	1.0	4.1	2.6
	4Xq	1	3	2.9	1	3	1.9		4Xq						
									4Xs				0.5	2.5	1.6
									5Zj	0.4	3.5	3.7	0.4	3.5	2.2
								4Xn	4Xp	3.5	25.4	35.0	5.6	41.3	45.6
									4Xr	2.8	17.6	24.3	2.8	17.6	19.5
									4Xs	0.5	3.4	4.7	0.5	3.4	3.8
									5Zj	0.9	8.3	11.4	0.9	8.3	9.1
									5Zm	1.2	16.6	22.9	1.2	16.6	18.3
4Xo	4Xm	3	11	0.6	4	15	0.7	4Xo	4Xm	4.9	66.3	1.6	6.1	76.4	1.7
	4Xo	217	1981	99.4	228	2082	98.8		4Xo	316.1	3840.8	92.0	328.0	3990.9	89.7
									4Xp	11.1	107.0	2.6	16.0	169.0	3.8
									4Xq	18.5	116.7	2.8	18.5	116.7	2.6
									4Xs	0.5	11.1	0.3	0.5	11.1	0.2
									5Yb				2.9	25.7	0.6
	5Zj				1	10	0.5		5Zj	3.9	32.4	0.8	5.0	47.7	1.1
4Xp	4Xm	6	32	0.7	11	58	0.7	4Xp	4Xm	2.5	28.8	9.7	2.5	28.8	5.0
	4Xn	36	302	6.5	60	512	6.5		4Xn						
	4Xo	119	255	5.5	173	379	4.8		4Xo						
	4Xp	159	1304	28.2	305	2542	32.5		4Xp	15.7	163.2	54.8	28.0	290.5	50.3
	4Xq	123	878	19.0	191	1371	17.5		4Xq						
	4Xr	123	907	19.6	161	1192	15.2		4Xr						
	4Xs	68	602	13.0	121	1082	13.8		4Xs	0.5	11.1	3.7	3.8	33.9	5.9
	5Yb	18	57	1.2	29	92	1.2		5Yb	2.9	58.3	19.6	11.4	158.0	27.4
	5Yc	17	60	1.3	19	67	0.9		5Yc						
	5Yd	1	1	0.0	4	4	0.1		5Yd						
	5Yf	8	26	0.6	10	33	0.4		5Yf						
	5Yg	1	2	0.0	1	2	0.0		5Yg						
	5Yu				1				5Yu						
	5Zg	4	9	0.2	7	15	0.2		5Zg						
	5Zh	5	30	0.6	6	36	0.5		5Zh						
	5Zj	35	62	1.3	64	114	1.5		5Zj	3.5	28.1	9.4	5.4	41.7	7.2
	5Zm	8	42	0.9	21	116	1.5		5Zm	1.2	8.3	2.8	3.6	23.3	4.0
	5Zn	3	62	1.3	10	202	2.6		5Zn						
	5Zo				1	16	0.2		5Zo						
4Xq	4Xo	1	3	100.0	1	3	100.0	4Xq	4Xo						

continued

Table 3 (continued)

Release area	Recapture area	<12 months total: Number recaptured	<12 months total: Adjusted number	<12 months total: Percent	Total: Number recaptured	Total: Adjusted number	Total: Percent
4Xr	4Xn	1	9	5.9	1	9	4.7
	4Xp						
	4Xq	3	22	15.0	3	22	12.0
	4Xr	25	84	58.9	33	115	64.1
	4Xs	9	20	13.7	10	22	12.1
	5Yb	3	9	6.5	3	9	5.2
	5Yf				1	3	1.8
4Xs	4Xm				1	6	0.7
	4Xn	1	9	1.9	1	9	1.1
	4Xo	1	2	0.5	1	2	0.3
	4Xp	1	8	1.8	7	62	7.8
	4Xq	5	36	7.8	9	65	8.3
	4Xr	24	177	38.7	30	221	28.1
	4Xs	21	186	40.8	42	376	47.7
	5Yb	7	22	4.7	8	25	3.1
	5Yf				1	3	0.4
	5Zj				1	2	0.3
	5Zm	3	17	3.8	3	17	2.2
5Yb	4Xo				1	2	0.9
	4Xp	1	8	4.5	4	34	13.2
	4Xq	7	49	26.6	9	64	24.6
	4Xr	12	88	47.7	12	88	34.0
	4Xs	1	9	4.7	4	36	13.7
	5Yb	9	27	14.6	9	27	10.4
	5Yc	1	4	1.9	1	4	1.4
	5Zm				1	5	1.8

Recapture area	Release area	Total: Number recaptured	Total: Adjusted number	Total: Percent	<12 months total: Recapture recaptured	<12 months total: Release number	<12 months total: Percent
	4Xm	1.2	7.2	3.7	1.2	7.2	2.7
	4Xp	11.9	50.7	25.7	17.7	75.7	28.0
	4Xr	8.4	34.7	17.6	8.4	34.7	12.9
	4Xs	2.7	11.1	5.6	4.9	20.9	7.7
	5Yb	20.0	77.4	39.2	25.7	104.3	38.6
	5Zj	3.3	16.1	8.1	4.8	27.0	10.0
4Xr	4Xn						
	4Xp	11.4	42.2	7.2	14.9	60.9	9.1
	4Xq						
	4Xr	81.2	351.5	59.8	92.4	400.3	59.8
	4Xs	13.5	53.9	9.2	16.3	66.2	9.9
	5Yb	34.3	138.6	23.6	34.3	138.6	20.7
	5Yf						
	5Zj	0.2	0.9	0.6	0.6	2.4	0.4
4Xs	4Xm						
	4Xn						
	4Xo						
	4Xp	6.3	56.8	10.1	11.2	100.9	14.6
	4Xq						
	4Xr	25.2	259.7	46.0	28.0	285.4	41.3
	4Xs	17.3	137.1	24.3	22.8	191.1	27.7
	5Yb	11.4	107.4	19.0	11.4	107.4	15.5
	5Yf						
	5Zj	0.4	3.9	0.7	0.6	5.8	0.8
	5Zm						
5Yb	4Xo						
	4Xp	1.7	13.7	4.1	2.7	22.5	6.5
	4Xq						
	4Xr	8.4	114.6	34.5	8.4	114.6	33.1
	4Xs	3.8	26.7	8.0	4.3	31.5	9.1
	5Yb	25.7	162.0	48.8	25.7	162.0	46.8
	5Yc						
	5Zm	1.2	15.3	4.6	1.2	15.3	4.4
5Yc	4Xp	1.6	5.1	36.6	1.8	5.7	39.1
	5Yb	2.9	8.9	63.3	2.9	8.9	60.7
5Yd	4Xp	0.1	0.1	30.9	0.4	0.4	50.0
	5Zj	0.2	0.2	61.6	0.4	0.4	50.0
5Ye	5Zj	0.2	0.2	100.0	0.2	0.2	100.0
5Yf	4Xp	0.7	1.8	74.5	0.9	2.3	21.3
	4Xr				2.8	6.4	60.2

continued

Table 3 (continued)

Release area	Recapture area	<12 months total: Number recaptured	<12 months total: Adjusted number	<12 months total: Percent	Total: Number recaptured	Total: Adjusted number	Total: Percent
5Zj	4Xm	2	10	1.1	2	10	0.7
	4Xn	5	41	4.7	5	41	2.9
	4Xo	21	43	4.9	27	58	4.0
	4Xp	17	136	15.6	29	248	17.3
	4Xq	18	121	13.9	26	193	13.5
	4Xr	1	7	0.8	3	22	1.5
	4Xs	2	17	1.9	3	27	1.9
	5Yd	1	1	0.1	2	2	0.1
	5Ye	1	2	0.2	1	2	0.1
	5Yf	1	3	0.4	1	3	0.2
	5Zg	1	3	0.3	1	3	0.2
	5Zh	3	19	2.2	3	19	1.3
	5Zj	206	387	44.5	325	609	42.6
	5Zm	15	82	9.4	18	100	7.0
	5Zn				5	95	6.7
5Zm	4Xn	1	8	12.0	1	8	8.5
	4Xp	1	8	11.6	3	29	31.7
	4Xs						
	5Yb	1	3	5.0	1	3	3.6
	5Zg				1	6	6.0
	5Zj	23	46	71.3	23	46	50.3

Recapture area	Release area	<12 months total: Number recaptured	<12 months total: Adjusted number	<12 months total: Percent	Total: Recapture recaptured	Total: Release number	Total: Percent
	4Xs				0.5	1.4	12.7
	5Zj	0.2	0.6	27.0	0.2	0.6	6.0
5Zg	4Xp	0.4	0.7	47.0	0.6	1.2	8.3
	5Zj	0.2	0.8	51.8	0.2	0.8	5.5
	5Zm				1.2	12.1	85.8
5Zh	4Xp	0.5	2.4	41.3	0.6	2.9	45.5
	5Zj	0.6	3.5	59.2	0.6	3.5	54.6
5Zj	4Xm						
	4Xn						
	4Xo				1.4	3.2	1.8
	4Xp	3.2	6.1	4.8	5.9	11.0	6.2
	4Xq						
	4Xr						
	4Xs				0.5	1.0	0.6
	5Yd						
	5Ye						
	5Yf						
	5Zg						
	5Zh						
	5Zj	39.6	72.2	56.6	60.1	112.0	63.3
	5Zm	27.3	49.1	38.5	37.3	49.1	27.8
	5Zn						
5Zm	4Xn						
	4Xp	0.7	3.4	7.2	1.9	12.6	20.9
	4Xs	1.6	15.0	31.4	1.6	15.0	24.8
	5Yb	2.9	14.0	29.4	2.9	14.0	23.3
	5Zg						
	5Zj	3.0	15.2	31.9	3.3	18.6	30.9
5Zn	4Xp	0.4	4.2	62.4	0.9	12.1	56.4
	5Zj	0.2	2.5	37.3	0.9	9.3	43.4
5Zo	4Xp				1.0	16.0	99.9

covered there and between 15% and 20% of recaptures were from releases in the 5Yb area. Cod tagged in unit area 4Xs show more widespread dispersal than those from 4Xr.

The small number of releases from division 5Y precluded detailed interpretation of movement. However, there is an indication of association with the 4X area, as well as movement from the Browns Bank area into 5Y, both of which were not unexpected because the majority of releases were near the northeastern border of 5Y. Results, therefore, probably do not reflect those for the remainder of the 5Y area.

The pattern observed for Georges Bank is similar to that seen on Browns Bank. Dispersal of postspawning cod appears to be substantial in both a north and south direction. Interaction between the Browns Bank and inshore area and Georges Bank accounted for most of the movement of tagged cod. The interchange was bidirectional, but more cod appeared to move from Georges Bank to Browns Bank (about 30%) compared with about 3% of Browns Bank cod moving to Georges Bank. Relatively small numbers of cod released in the 5Zj and 5Zm area were recaptured in areas further to the south or west. However, Hunt and Buzeta (1996) noted that the U.S. commercial fishery, and therefore the probability of recovering tags from the 1994 and later releases in the area west of the IMB, has been substantially reduced with the introduction of closed areas in 1995.

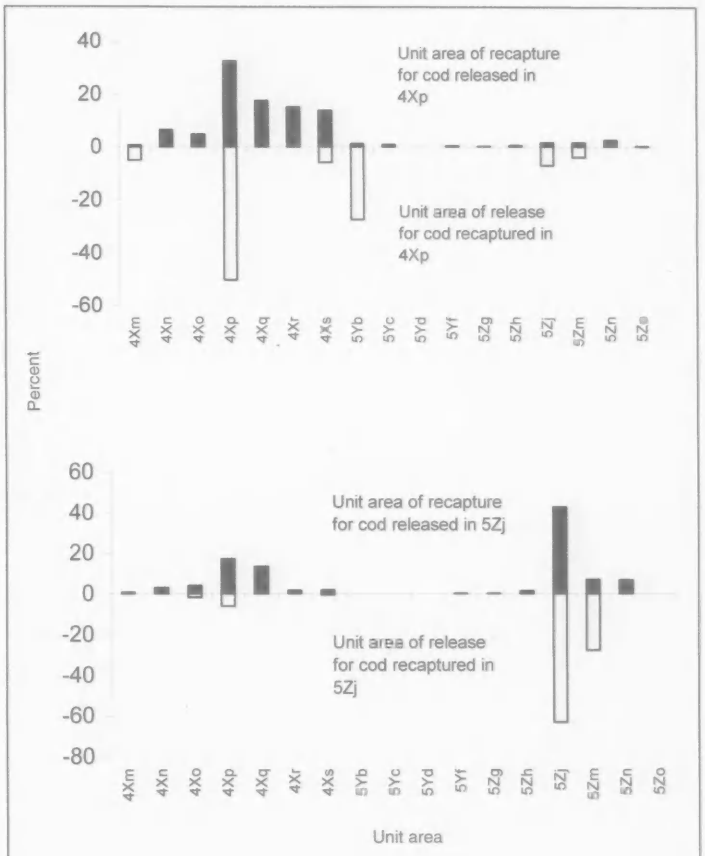


Figure 6

Summary of adjusted cod tag recoveries for the Browns Bank (4Xp) and Georges Bank (5Zj) areas, aggregated by unit area.

Information for the Browns Bank and Georges Bank areas is shown in Figure 6 for adjusted recaptures in the area and from the area. Preliminary comparison of recoveries in the first twelve months and total recoveries showed little variation in the distribution or proportions (Table 3) and therefore total recoveries were used. Dispersal from the area of release appears to be substantial for both the 4Xp and 5Zj areas. However, a high proportion of fish recaptured in the two areas was released from the same area. The two patterns may represent postspawning dispersal (top panel for each area) and summer distribution or year-round residents (bottom panel for each area).

The seasonal distribution of recaptures from the Browns Bank and Georges Bank areas is shown in Figure 7. Recaptures were combined by quarter and unit area (by division for recaptures outside the division of release). In the Browns Bank area, seasonal distribution appears to be consistent with aggregation in the spawning season (first quarter) and with progressive dispersal to adjacent areas in the remainder of the year. This pattern may be repeated on an annual basis with return of migrants during the spawning season. Seasonal trends in the Georges Bank area are more difficult to interpret and the influence of fishing season may be a factor, compared with trends for Browns Bank, because closure to commercial groundfishing in the first half of the year limits potential recoveries during the spawning season. However, the recapture pattern for cod recovered in division 4X suggests that the migrants do not return to Georges Bank because the proportion remains relatively constant over the first to third quarters and increases in the fourth quarter.

Figures 8 and 9 provide information on the spatial dispersal of cod tagged in the Browns Bank and Georges Bank areas with adjusted recoveries aggregated by 10-min squares and expressed on a per thousand basis. Most recoveries were made near the respective release site. When movement occurred, a general pattern of dispersal from the release site with a gradient from the tagging site to the edges of the distribution was evident. Intermediate areas of aggregation were consistent with the geographic distribution of fisheries effort and associated probability of recapture. Interchange occurred between release site areas, but the main vector of movement from both sites was towards the northeast. As a result, most long distance recoveries were made in the southwestern Nova Scotia and Bay of Fundy inshore areas, although there was limited movement into the northwestern Gulf of Maine or western Georges Bank areas.

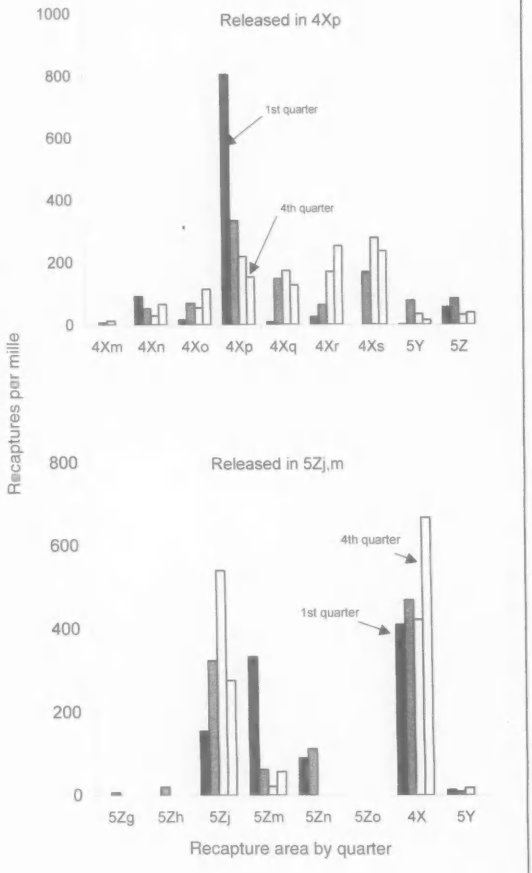


Figure 7

Quarterly distribution of cod tag recoveries from the Browns Bank (4Xp) and Georges Bank (5Zj) release areas, aggregated by unit area.

The two time periods associated with Georges Bank tagging are compared in Figure 10 for the 1994 and 1984–85 experiments. The two distributions are similar and both show the majority of cod remaining near the release area; more of the long distance dispersion occurred into the 4X area than to the west into the inner Gulf of Maine. Similarity in the results from the two time periods indicates some consistency in the northeast vector of movement. However, a higher proportion of cod were recaptured in 4X from the 1994 experiment (55%) compared with the earlier releases (42%). As noted above, the reduced U.S. commercial fishery in the area west of the IMB since 1995 also reduced the probability of tag recaptures from the 1994 experiment in this area.

The distribution of recaptures and elapsed time for the February and March releases for unit areas 4Xp (Browns Bank) and 5Zj (Georges Bank) are shown in Figure 11. The majority of returns in both areas occurred in the first 24 months after release, and the maximum time at large was 87 months (Table 4), but the overall average of time at large was less than 8 months. Many fish were recaptured in the first month after release, probably before postspawning dispersion had occurred. Maximum distance travelled was over 620 km and the mean distanced travelled was 60 km. Substantial numbers of cod moved hundreds of kilometres, indicating that cod can survive the stress of tagging and are capable of long distance movements. A strong seasonal pattern, consistent with the seasonal nature of the commercial fishery, is evident. The fishery on Browns Bank is typically year round, with peaks late spring and summer (Clark, 1996), and on Georges Bank, the fishery typically opens in June (Hunt and Buzeta 1996). The seasonal peaks in recaptures (4–6, 16–18, etc. months after February releases) coincides with the commercial fishing activity.

Length at the time of recapture was available for a relatively small proportion of recaptures. For these samples, the net increase in length and elapsed time was used to calculate a specific growth rate, expressed as annual rate, for each unit area. Results are given in Table 5 for 10-cm length-at-release intervals but sample size was small for all but the 4Xp, 4Xs, and 5Zj areas. The calculated annual growth rates indicate differences between areas and follow an expected pattern of decrease as the length at release increases. Of these three areas, the Georges Bank area had the fastest growth with an annual increase of about 19 cm for cod released as 40-cm

individuals. Estimates of growth rates from this study are consistent with the more extensive study on cod growth completed by Shackell et al. (1997).

Discussion

Fisheries management objectives for either conservation or yield from a defined management unit are usually based on a closed system approach that requires that emigration and immigration of fish from adjacent stocks be sufficiently low so as to avoid confounding stock-status evaluations. Gulland's (1983) operational definition of a stock also considered interchange between stocks and he suggested that it can be ignored if conclusions on the population dynamics of the stock remain valid. Therefore, two problems require evaluation in assessing stock definitions: 1) Is there evidence of interchange of fish at a geographic scale larger than the one used to define a stock boundary? and 2) If interchange does occur, what are the impacts on population dynamics and on the assumptions used in models to estimate population parameters?

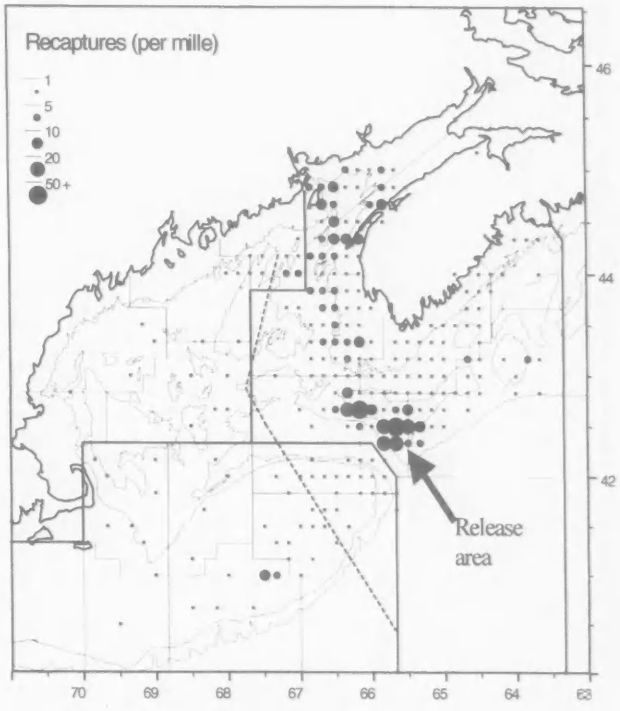


Figure 8

Distribution of adjusted cod tag recoveries from releases in the Browns Bank (4Xp) area, aggregated by 10-min latitude and longitude squares.

Tagging experiments can address the first of the two questions provided that the study logistics have not compromised the results and that both ongoing fisheries removals and management activities during the recapture period do not invalidate interpretation of the results. Capture, tagging, and release of cod with bottom trawl methods and T-bar tags can generate a large number of releases and, according to a relatively high recapture rate and extended time at large, appear to result in nominal tag- or stress-induced mortality. During the 1994 experiment, cod tagged from one tow were recaptured in a subsequent tow, either the same day or several days later and thus may indicate that tagged cod resume a normal schooling pattern shortly after release. Efficiency of the tagging operation is also a contributing factor as is the time of year, depth, and condition of tagged fish. Clay et al. (1989) reported on tagging experiments under winter conditions and concluded that cod at this time of year have a better chance of surviving the tagging process. Tag loss was not examined in our study but Saunders et al. (1990), in a study of sablefish tagged with tags similar to those used in our study, concluded that tag loss could be as high as 10% in the first year and 2% per year thereafter. Less than 10% of cod tagged with T-bar tags for identification in a live-fish holding facility experienced tag loss in the first week, although losses were higher after biweekly netting and sampling for length and weight observation (Nelson[1]).

In the present study, the influence of high annual mortality rates (Z), failure to report recaptures, and the effectiveness of advertisements and rewards, the impact of fishery controls, and the potential bias between Canada and U.S. reporting rates may be more substantial than factors such as tag loss. However, these variables are difficult to quantify.

All cod stocks in the study area have been subjected to very high exploitation rates in the last decade. For example, Hunt and Buzeta (1996) reported rates of over 40% in the 1990s for the Georges Bank cod stock. A similar capture rate applied to the tagged population [N] could result in an apparent rate [R] of over 20% returns after accounting for tagging mortality (~20%) and tag loss (~10%) and assuming full reporting [$R = 0.4(N - N(0.2 + 0.1) = 0.28N$]. Observed return rates were less than half those for the Georges Bank and Browns Bank areas and a lack of reporting could be a contributing factor. Anecdotal information from field staff working in fishing ports

[1] Nelson, C. 1996. Department of Fisheries and Oceans, St. Andrews, New Brunswick, Canada. Personal. commun.

indicates that some fishermen with tags did not return them because of resistance to identifying fishing locations and because of preconceived ideas and concerns about the significance of the release and recapture site. The extent of a lack of reporting is difficult to quantify and its effect may not introduce bias if nonreported tags have the same geographic distribution as reported tags.

Advertizing campaigns for the 1994 experiment were much more extensive than those used in the early 1980s. Printed notices covered a larger audience, the experiment was discussed with industry representatives and conducted with their support, interim results were presented, and a more active role was taken by field staff to collect recovered tags. However, the return rate was higher in the 1980s. For example, the return rate in the first 24 months for the 1984–85 Georges Bank experiments was about 12.2% compared with 5.5% for the 1994 experiment.

Fisheries management controls may play a more substantial role in determining the number of recaptures. Controls may include area closures, restricted seasons, and catch limitations. The Browns Bank area has been closed to fishing during the winter spawning season for many years. Canadian commercial fishing on Georges Bank has been closed between January and May since 1994, and the United States has an extensive closed area covering most of the northeast part of the Bank. These restrictions substantially reduce the possibility of recaptures during the spawning season.

The establishment of the International Maritime Boundary in 1984 between the United States and Canada and the associated opinions and concerns of the fishing industry have undoubtedly introduced bias in the tag return rate and perhaps in the reported recovery location. It might be assumed that the direction of the bias would tend to support the concept of national ownership of the resource by the fishing industry and that tags recovered at times or locations that appeared to contradict this opinion would be withheld or discarded. Comparison of tag recoveries from the 1984–85 releases with those from the 1994 releases does not show substantial differences in distribution of fish. The first period includes the time when response to international boundary change would have been most sensitive and pronounced. The second period, more than ten years after the change, might be expected to have reduced concerns by fishermen on tag location. However, the impact of nonreporting bias would be of most concern in evaluating the proportional spatial distribution of tag recoveries. Bias in reported recapture location is of less concern because fishing activities are monitored and there is limited opportunity to misreport the area of operations.

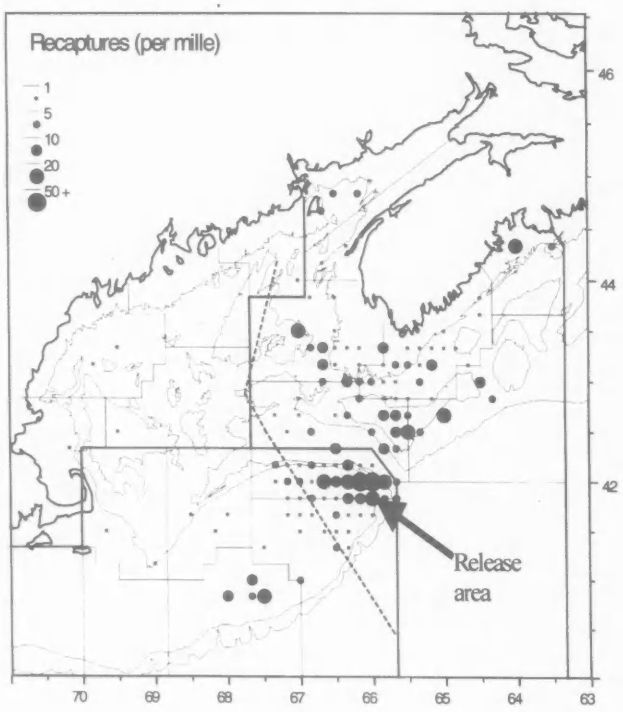


Figure 9

Distribution of adjusted cod tag recoveries from releases in the Georges Bank (5Zj) area, aggregated by 10-min latitude and longitude squares.

Total allowable catches and landings of cod from the Georges Bank area in 1994 declined to less than 50% of the recent ten-yr average and are expected to remain at low levels for a number of years (Hunt and Buzeta, 1996). The impact of reduced catches is accounted for, to some extent, by reduced annual exploitation and its impact on tag-recapture adjustment. However, other changes in the fishery, such as shifts in gear sectors and spatial redirection of effort, may offset this adjustment.

Even with the need, discussed above, to qualify the interpretation of tagging data, we believe the results of the present study clearly indicate that interchange between the 5Zj,m and 4X cod management units occurs with a net movement from 5Zj,m to 4X. Cod released on Georges Bank exhibited movement outside the 5Z management area onto Browns Bank and the inshore areas of Nova Scotia and the Bay of Fundy. Cod released on Browns Bank also moved to the inshore area of Nova Scotia

as well as onto Georges Bank. These results correspond to those of historical studies, although conclusions from the earlier studies may be more limited in scope owing to the smaller number of released fish and the lower intensity of commercial fisheries at the time. In his review of tagging results from the late 1890s to the 1960s in the Gulf of Maine, Wise (1963) concluded that cod of the offshore areas of Browns and Georges Banks were closely related to fish of the southwestern Nova Scotia area. Wise and Jensen (1960) had earlier concluded that the eastern Georges Bank cod population mixed little with the more western or southern components and interacted primarily with the southwestern Nova Scotia area. Templeman (1962) in summarizing cod tagging information for the northwest Atlantic concluded that there were discrete spawning stocks on the eastern part of Georges Bank and Browns Bank and mixing in both directions across the Fundian Channel as well as to inshore areas. Results of tagging studies completed in 1969 on Browns Bank and in 1972 from inshore areas of Nova Scotia were reported by Halliday (1973) and he concluded that there was a separation of inshore and offshore stocks. McKenzie (1956) and McCracken (1956) tagged cod in the inshore area of southwest Nova Scotia and observed limited interchange with the offshore banks and the Bay of Fundy. They concluded that the resident inshore cod stocks in the Bay of Fundy and southwestern Nova Scotia were relatively stationary. They also explained the offshore recaptures of cod tagged in the inshore area as evidence that cod from more migratory stocks could be present in inshore areas at certain times of the year.

Hunt and Buzeta (1989) provide details of the basis for partitioning the northeast part of Georges Bank (5Zj,m) as a separate Canadian management unit distinct from the remainder of the 5Zw+SA6 area. They concluded that spatial distribution from tagging studies and other biological characteristics were sufficiently distinct to define the 5Zj,m area as a management unit that could be expected to benefit from management controls. However, the 5Zj,m area is partitioned by the IMB so that commercial fisheries by Canada and the United States are limited to their respective sides. Gavaris et al. (1993) conducted an analysis of cod movement in relation to the IMB using commercial catches and research sur-

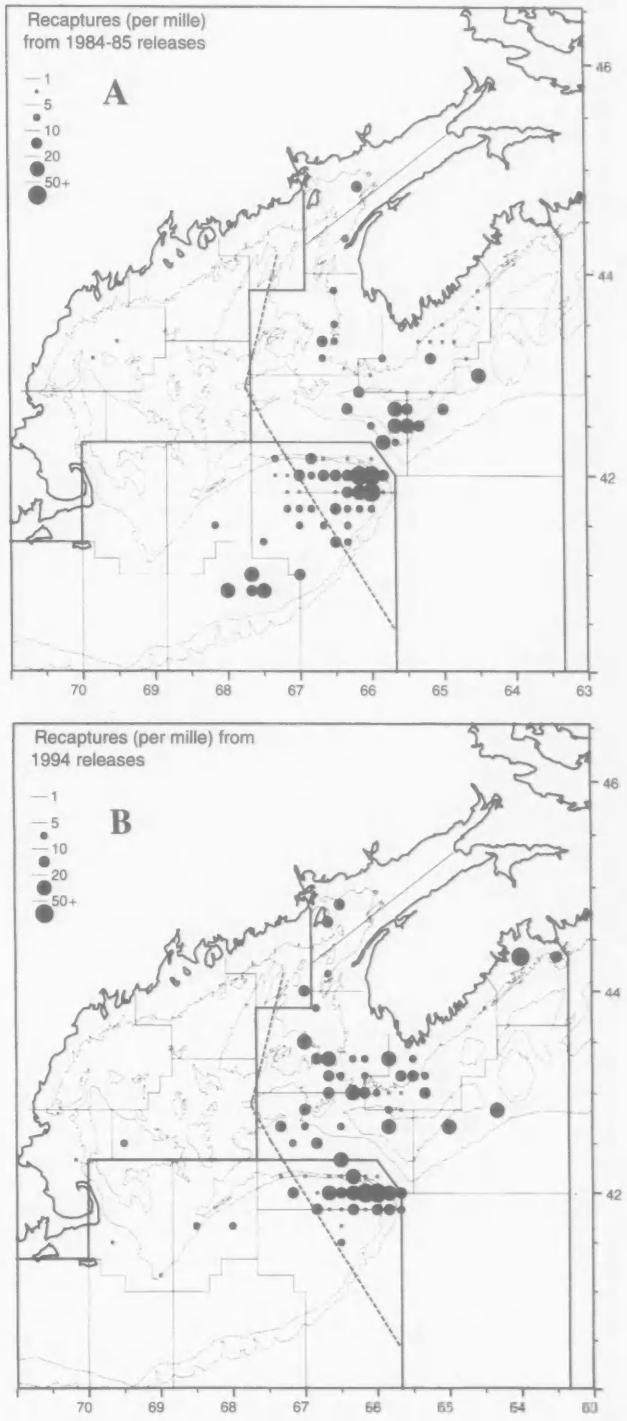


Figure 10

Distribution of adjusted cod tag recoveries from releases in the Georges Bank (5Zj) area, aggregated by 10-min latitude and longitude squares: (**A**) 1994 releases; (**B**) 1984–85 releases

Table 4

Summary by unit area of release of months after release to recapture and distance travelled (km).

Area of release	Months after release			Distance travelled		
	Minimum	Maximum	Average	Minimum	Maximum	Average
4Xm	0	87	12.0	1.1 2	385	64.5
4Xo	0	25	2.4	0	448	7.2
4Xp	0	62	12.2	2	626	128.6
4Xq	7	7	7	24	24	24.0
4Xr	0	28	4.4	0	235	25.4
4Xs	0	38	8.5	0	385	75.8
5Yb	0	31	7.0	2	221	66.5
5Zj	0	65	10.1	2	367	62.3
5Zm	3	16	5.3	22	265	93.4
Average	0	39.9	7.6	5.9	328.6	61.0

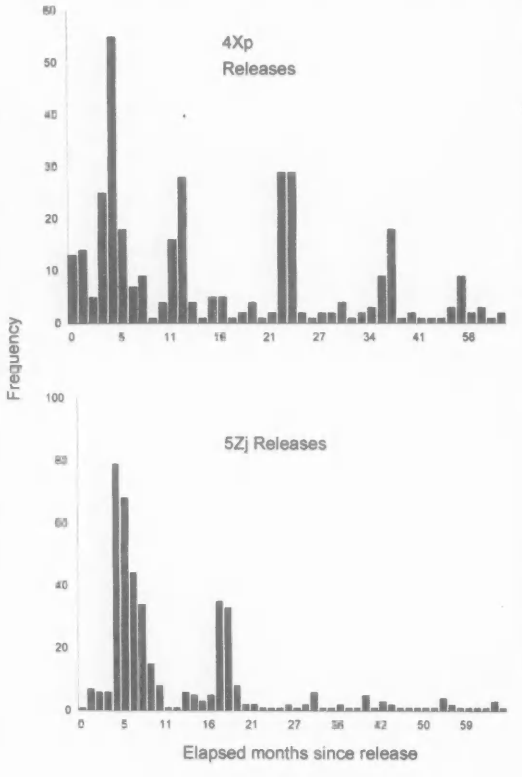


Figure 11

Summary of adjusted cod tag recoveries for releases in the Browns Bank (4Xp) and Georges Bank (5Zj) areas by elapsed time from release to recovery, in months.

vey indices. They concluded that extensive movement does occur with a strong seasonal pattern in which almost 100% of the biomass is on the Canadian side in the fall–winter period and about 65% in the spring–summer period. Results of the present study support the occurrence of seasonal movement but also indicate that it is not a closed system. There is evidence of immigration and emigration and an apparent net loss from the Georges Bank area to the Browns Bank and division 4X area.

In division 4X, two substocks (Bay of Fundy and Scotian Shelf) are already assumed (Clark, 1996) with distinct growth characteristics. However, tagging results show interchange between the Bay of Fundy, the inshore areas of southern Nova Scotia, and Browns and Georges Banks. The greatest exchange occurs between the offshore Browns Bank area and the inshore areas and the Bay of Fundy. Our results indicate that the extent of movement by cod in the Gulf of Maine area is substantial and that it crosses the present stock boundaries between 4X, 5Y, and 5Z. The interchange appears to be primarily between the eastern part of Georges Bank (the Canadian management unit) and 4X. Although movement between 4X and 5Y was observed, the number of releases and recaptures was small and the tagging location was close to the boundary between these areas. Exchange between 5Z and 5Y also occurs but at a relatively low rate.

Investigation of the potential impact of cod movement between stocks on models used for population estimates will require further work. Interpretation of diagnostics for population models such as ADAPT (Gavaris, 1988) from a stock concept might give

Table 5

Growth rate of cod estimated from net increase in length and elapsed time, expressed as an annual rate. Number of observations are shown in parentheses.

Release length (cm)	4Xm	4Xo	4Xp	4Xr	4Xs	5Yb	5Zj
20–29	12.5 (2)	12.0 (4)					
30–39	13.4 (7)	14.9 (6)		17.7 (8)	26.6 (4)		
40–49	7.9 (7)	8.9 (8)	12.4 (7)		15.8 (15)	33.8 (5)	18.9 (16)
50–59	10.7 (22)	8.0 (4)	9.2 (28)	2.6 (3)	15.8 (16)	30.7 (3)	16.9 (12)
60–69	5.1 (4)		7.5 (66)	18.0 (2)	10.8 (18)	18.9 (9)	12.2 (45)
70–79			6.7 (88)	6.0 (1)	4.8 (7)	21.0 (2)	11.9 (26)
80–89			5.7 (46)			4.0 (1)	7.2 (18)
90–99			3.7 (14)				5.8 (11)
100–109			3.1 (3)				6.9 (2)

some indication of the need for revising model formulations. For example, changes in apparent natural mortality or unexplained changes in fishing mortality could be evaluated as the result of losses due to emigration or increases due to immigration. However, stock definition may be further confounded if cod movements have a temporal element and shifts in distribution occur without permanent loss or gain.

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Growth analysis of striped mullet, *Mugil cephalus*, and white mullet, *M. curema* (Pisces: Mugilidae), in the Gulf of Mexico

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Abstract.—The parameters from von Bertalanffy's growth equation were estimated for *Mugil cephalus* and *M. curema* located in Tamiahua coastal lagoon in Veracruz, México. Also differences in growth and longevity between sexes were obtained. The following were growth parameters for *M. cephalus*: L_∞ = 642.4 mm, W_∞ = 2,352.12 g, k = 0.099, t_0 = –2.85, ($A_{0.95}$) = 28.3 years; and for *M. curema*: L_∞ = 461.4 mm, W_∞ = 844.73 g, k = 0.14 y t_0 = –3.62, ($A_{0.95}$) = 18.7 years. Some important differences among growth rates from other areas were found. Significant differences in the growth rate between sexes were observed. The following were growth parameters for *M. cephalus*: females: L_∞ = 622.9 mm, k = 0.107, t_0= –2.67; $A_{0.95}$ = 26.2 years; males: L_∞ = 603.9 mm, k = 0.105, t_0 = –2.98; $A_{0.95}$ = 26.5 years; for *M. curema*: females: L_∞ = 454.6 mm, k = 0.135, t_0 = –3.94; $A_{0.95}$ = 19.2 years; males: L_∞ = 411.8 mm, k= 0.187, t_0 = –3.03; $A_{0.95}$ = 14.0 years.

The striped mullet, *Mugil cephalus* (Linnaeus, 1758), has a worldwide distribution, between 42°N and 42°S (de Silva, 1980), whereas the white mullet, *Mugil curema* (Valenciennes, 1836), is basically an American species found from Cape Cod, USA, to Brazil in the Atlantic and from Bahia Magdalena, Mexico, to Chile in the Pacific (Jordan and Everman, 1896). However, Alvarez (1976) has recorded *M. curema* off the western coast of Africa.

In Mexico, 99% of the commercial catch of these mullets takes place in the states of Tamaulipas, mainly in Laguna Madre and in Veracruz, and mainly in the Pueblo Viejo and Tamiahua. The mullet fishery constitutes one of the ten most important fisheries in Mexico as a result of its catch volume, which surpasses 10,000 metric tons (t) annually (Polanco et al., 1987).

These species provide both the meat and the roe, locally called "hueva," which commands a greater commercial price than the meat. Whereas striped mullet meat has a value of one US$ per kg, the roe is valued at seven US$ per kg. The female gonad has a widespread market because it is eaten regionally as well as nationally and internationally. In 1995 alone, 43 t of roe with a value of US$ 150,000 (at the present time US$ 800,000) were exported to the United States (Polanco et al., 1987).

Although these species of mullets represent an important source of food in many countries, studies on their ecology and population dynamics are insufficient. In Mexico some population parameters of *M. cephalus* in Tamiahua lagoon, Veracruz, have been analyzed by Marquez (1974) and Garcia (1980). Similarly, Diaz and Hernandez (1980) and Romero and Castro (1983) studied *M. cephalus* in the San Andres lagoon in Tamaulipas and in the Mar Muerto in Chiapas, respectively. Yañez-Arancibia (1976) analyzed some aspects of feeding habits, growth, and maturity of *M. curema* in the coastal lagoon system of Guerrero. Comparative studies on *M. curema* and *M. cephalus* in Tamiahua lagoon, Veracruz, were carried out by the following authors: Perez-Garcia and Ibañez-Aguirre (1992) and Ibañez-Aguirre and Lleonart (1996) on relative growth

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and comparative morphometrics; Ibañez-Aguirre and Gallardo-Cabello (1996a) on total and natural mortality and Sanchez-Rueda et al. (1997) on the analysis of sediments in stomach contents. On the international scene, the studies on *M. cephalus* by de Silva (1980), Perera and de Silva (1978), de Silva and Silva (1979) in a coastal lagoon in Sri Lanka, Drake et al. (1984) in the coastal lagoon of San Fernando Cadiz, Cech and Wohlschlag (1975) along the coast of Texas, Broadhead (1958) along the coast of Florida, and Thompson (1963) in Australia, are worthy of mention, as well as those carried out by Alvarez (1976, 1979 and 1981), Richards and Castagna (1976), and Phillips et al. (1987) on *M. curema* .

In view of the above studies, the purpose of this study was to carry out an in-depth analysis of the growth characteristics of *M. cephalus* and *M. curema* with respect to length, sex, weight, and longevity in Tamiahua lagoon, Veracruz, Mexico.

Material and methods

Specimens were obtained from the commercial catch landed near Tamiahua lagoon, Veracruz, Mexico (Fig. 1). The most commonly employed fishing nets were gill nets of 35-mm mesh size (knot-to-knot) for *M. cephalus* and 30-mm mesh size (knot-to-knot) for *M. curema* . Sampling was carried out monthly during the first 8 days of each month for a year, from April 1991 to March 1992.

Figure 1
Map of the Tamiahua Lagoon, Veracruz, Mexico.

Total length (TL) was recorded from 2628 specimens of *M. cephalus* and 3354 of *M. curema* . For the study of growth, two independent readers examined scales, and otoliths (right sagitta) from 232 specimens of *M. cephalus* (122 females and 110 males) ranging from 200 to 400 mm and 292 specimens of *M. curema* (148 females and 144 males) ranging from 180 to 330 mm. The scales were cleaned, placed between two glass slides, and observed with transmitted light. The otoliths were submerged in a petri plate in xylol as a clarifying liquid and observed through a stereoscopic microscope with transmitted light. The analysis of the annual frequency variation of the fast growth rings (opaque) and slow growth rings (hyaline) of the margin of the otoliths showed that each year, one fast growth band and one slow growth band are deposited in the otoliths of boths species of mullets (Ibañez-Aguirre and Gallardo-Cabello, 1996b). It was reported earlier that otoliths give better results than do scales for the age determination of both species and make possible a definition of five age groups for *M. cephalus* and six for *M. curema* (Ibañez-Aguirre and Gallardo-Cabello, 1996b). These average lengths were used to obtain the constants for the von Bertalanffy equation (Table 1).

Ages "0" and "1" were not collected for *M. cephalus*, as a result of the mesh size of the nets; instead they were obtained by using the back-calculation method of Lea (1910, in Francis, 1990) and Bagenal and Tesch (1978, in Francis, 1990).

The constants for the von Bertalanffy equation (1938), L_∞, k, and t_0, were obtained by using the combined method of Ford (1933) and Walford (1946), and the methods of Gulland (1964), Tomlinson and Abramson (1961), Allen (1966), Beverton[1], Prager (1987), and Bayley (1977). Growth was also measured for each sex of both species. Growth curves for both species were obtained from the constants of the equation calculated by the above mentioned methods. The sum of the squared differences (Σe_i^2) was used to compare the differences between calculated and observed values.

Hotelling's T^2 test (Bernard, 1981) was used to compare growth curves of the two sexes of both species. This test assumes that estimations of L_∞, k, and t_0 for both groups were obtained from two normal

[1] Beverton, R. J. H. 1954. Notes on the use of theoretical models in the study of the dynamics of exploited fish populations. U.S. Fish Wildl. Serv., Fisheries Laboratory, Beaufort, Misc. Contrib. Rep., 181 p.

Table 1

Mean length (mm) employed for obtaining the growth parameters.

	Mugil cephalus					*Mugil curema*				
Age	Females (±SD)	Males (±SD)	Species (±SD)	*n*	Calculated values (±SD)	Females (±SD)	Males (±SD)	Species (±SD)	*n*	Calculated values (±SD)
"0"	156[1] (± 9)	160[1] (± 13)	158[a] (± 11)	0	158.34 (± 9)	187 (± 10)	176 (± 11)	183 (± 4)	4	184.20 (±9)
"1"	203[1] (± 7)	207[1] (± 9)	204[a] (± 7)	0	204.09 (± 9)	224 (± 8)	221 (± 9)	223 (± 7)	60	220.56 (± 11)
"2"	246 (± 5)	247 (± 19)	246 (± 14)	45	245.53 (±13)	251 (± 6)	250 (± 8)	252 (± 9)	71	252.15 (± 6)
"3"	283 (± 3)	281 (± 10)	282 (± 11)	59	283.04 (± 11)	276 (± 7)	276 (± 7)	278 (± 8)	66	279.60 (± 4)
"4"	319 (± 7)	315 (± 10)	317 (± 9)	44	317.01 (±11)	299 (± 6)	300 (± 4)	303 (± 7)	54	303.44 (± 3)
"5"	350 (± 9)	344 (± 8)	349 (± 12)	51	347.77 (± 8)	320 (± 4)	321 (± 4)	325 (± 8)	37	324.16 (± 4)
"6"	377 (± 8)	369 (± 6)	375 (± 12)	33	375.62 (± 11)	—	—	—		

[1] Average lengths obtained by back calculation.

Table 2

Estimates of the constants of the von Bertalanffy equation for *M. cephalus*, according to the different methods used.

	Species				Females				Males			
Method	L_∞(mm)	k	t_0	SD[2]	L_∞(mm)	k	t_0	SD[2]	L_∞(mm)	k	t_0	SD[2]
Walford-Gulland	637.97	0.0998	−2.8838	4.049	627.54	0.1052	−2.7342	2.186	609.05	0.1028	−3.0651	3.339
Beverton regression	637.97	0.1000	−2.8723	3.827	627.54	0.1053	−2.7281	2.110	609.05	0.1029	−3.0575	3.237
Tomlinson and Abramson	640.64	0.0998	−2.8418	3.211	627.24	0.1054	−2.7280	2.115	604.93	0.1043	−3.0376	3.341
Beverton regression	640.64	0.0998	−2.8400	3.211	627.24	0.1059	−2.6958	1.793	604.93	0.1050	−2.9860	2.725
Allen	642.00	0.0993	−2.8483	3.421	622.87	0.1074	−2.6709	1.794	603.52	0.1054	−2.9772	2.919
Beverton regression	642.00	0.0994	−2.8476	3.210	622.87	0.1074	−2.6697	1.783	603.52	0.1055	−2.9765	2.723
Prager	642.40	0.0993	−2.8480	3.210	622.90	0.1074	−2.6690	1.790	603.90	0.1054	−2.9770	2.722
Beverton regression	642.40	0.0993	−2.8499	3.209[1]	622.90	0.1074	−2.6699	1.782[1]	603.90	0.1054	−2.9791	2.722[1]
Bayley	640.00	0.1003	−2.8210	3.408	615.89	0.1094	−2.6620	2.382	608.34	0.1055	−2.8988	8.592

[1] The best fit.

distributions of joint probability, with three variables and one common variance.

The complete and eviscerated weights of 473 and 329 specimens of *M. cephalus* and *M. curema* , respectively, were recorded for the study of growth by weight. Weight data were recorded for each 20-mm length interval and the average weight for each size class was calculated.

The function $W = aL^b$ was used to obtain the weight-length relationship. Data for growth by length and the weight-length relationship were used to obtain the weight for each age. Growth by weight was obtained by substituting L_t and L_∞ by W_t and W_∞, respectively, obtained from the weight-length relationship in the von Bertalanffy equation. Taylor's equation (1958, 1960) was used to calculate age limit or longevity (95% of L_∞).

Results

Growth in length

Mugil cephalus The values for L_∞ and k were very similar (Table 2). The method that provided the greatest differences was that of Ford (1933) and Walford (1946). This similarity was due to the obtention of these constants; the t_0 value determined by Gulland

(1964) was also employed. Gulland recommends using just the age groups that are best represented and thus avoids errors due to a low representation of some poorly sampled age groups. Some calculations were repeated and the following t_0 values were obtained for the 3–5 years age groups: –2.74 (females), –3.07 (males), –2.89 (both species, sexes combined); and for the 3–6 age groups: –2.67 (females), –2.98 (males), –2.85 (both species, sexes combined).

The best fit was found with the t_0 result calculated for 3–6 years age groups. Thus, these values were used to obtain the average t_0 (Table 2). Use of the Beverton[1] equation improved the calculated values in comparison with the values observed by Ford (1933) Walford (1946), Tomlinson and Abramson (1961), Allen (1966), Bayley (1977), and Prager (1987) methods.

The calculated curve that best fitted values observed through otoliths corresponded to the parameters that were calculated with the Prager (1987) method and fitted with the Beverton[1] equation (Table 2). The calculated values of the lengths for different ages as well as their standard deviation (SD) were obtained by using these parameters for the two species (Table 1) which are consistent and, in general, show improved calculated values. Figure 2 presents the theoretical growth curve for *M. cephalus* ages 0–6 years.

During the first two years of life, striped mullet grew rapidly in length, with average increases of 45.8 mm during the first year and 41.4 mm during the second. From the third year on, growth decreased to annual increases in total length of 37.5 mm. Increases between the third and fifth years varied from 34.0 to 30.8 mm. Between the fifth and sixth years the increase was even smaller, with an average increase of 27.8 mm. In general, growth was high during the first two years of life and then decreased. This decrease is probably related to the time of first sexual maturity, which for this species occurs from 280 to 299 mm TL (males and females, respectively), which corresponds to an age of 3 years in both cases (Ibañez-Aguirre and Gallardo-Cabello, 1996b). L_∞ and k have a negative correlation, whereas L_∞ is high, the growth rate is low (Table 2).

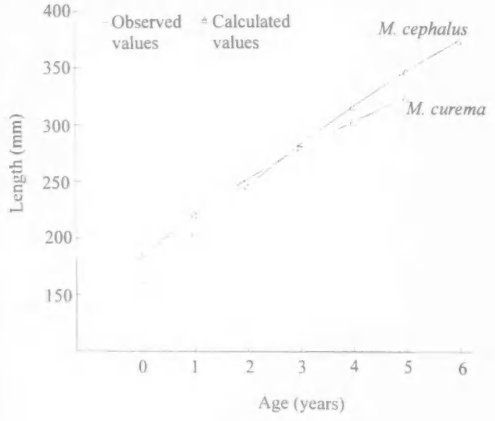

Figure 2
Theoretical growth curve for *M. cephalus* and *M. curema*.

Mugil curema As can be seen in Table 3, L_∞ and k values obtained with the Ford (1933) and Walford (1946) method show the greatest difference with respect to the values calculated by the Tomlinson and Abramson (1961), Allen (1966), Prager (1987), Beverton,[1] and Bayley (1977) methods.

As with *M. cephalus* , new calculations for the t_0 value were made by using the Gulland (1964) method for the 1–4, 3–5, and 2–4 years age groups; the following t_0 values were obtained: for the 1–4 years age groups –3.94 (females), –3.03 (males), –3.62 (both species, sexes combined), for the 3–5 years age groups: –3.73 (females), –2.77 (males), –3.41 (both species, sexes combined) and for the 2–4 years age groups –3.72 (females), –2.75 (males), –3.39 (both species, sexes combined).

The von Bertalanffy curves showed the best fit for the calculated values of the 1–4 yr age groups. These values were used to obtain average t_0. The Beverton[1] equation with the above methods improved calculated values only in the case of the Ford (1933) and Walford (1946) method. The calculated curve that best fitted observed values through otoliths corresponded to the parameters calculated with the Prager (1987) method, as can be seen in Table 3.

Using these parameters, we calculated values for lengths at different ages, as well as their SD, which, as in the case of *M. cephalus*, are consistent and, in general, show improved calculated values (Table 1). Figure 2 presents the theoretical curve for growth in length of *M. curema* , for the ages of 0–5 years.

A high increase in length was recorded during the first year, after which growth decreased markedly. Size increased by 27.5 mm TL between the second and third years, 23.8 mm between the third and fourth years, and 20.7 mm between the fourth and fifth years. The decrease in growth from the first year on is related to the first sexual maturity, which in this species occurs in small sizes from 181 to 208 mm TL for males and females, respectively, at ages "0" and "1" (Ibañez-Aguirre and Gallardo-Cabello, 1996b).

Table 3

Estimates of the constants of the von Bertalanffy equation for *M. curema*, according to the different methods employed.

	Species				Females				Males			
Method	L_∞(mm)	k	t_0	SD²	L_∞(mm)	k	t_0	SD²	L_∞(mm)	k	t_0	SD²
Walford-Gulland	450.35	0.1511	–3.4372	14.921	444.98	0.1446	–3.7568	11.144	402.75	0.2026	–2.8121	30.593
Beverton regression	450.35	0.1494	–3.5039	11.547	444.98	0.1430	–3.8259	8.479	402.75	0.2000	–2.8816	23.712
Tomlinson and Abramson	458.44	0.1427	–3.5976	10.895	454.13	0.1358	–3.9352	8.041	411.99	0.1863	–3.0272	21.688
Beverton regression	458.44	0.1430	–3.5875	10.944	454.13	0.1360	–3.9283	8.057	411.99	0.1869	–3.0116	21.825
Allen	461.37	0.1406	–3.6238	10.866	454.58	0.1354	–3.9413	8.054	411.85	0.1865	–3.0256	21.688
Beverton regression	461.37	0.1408	–3.6167	10.885	454.58	0.1356	–3.9332	8.053	411.85	0.1871	–3.0097	21.830
Prager	461.40	0.1406	–3.6240	10.864[1]	454.60	0.1355	–3.9400	8.040[a]	411.80	0.1865	–3.0260	21.682[1]
Beverton regression	461.40	0.1408	–3.6170	10.885	454.60	0.1356	–3.9334	8.053	411.80	0.1872	–3.0090	21.833
Bayley	455.79	0.1451	–3.5559	11.134	449.60	0.1390	–3.8953	8.127	406.54	0.1931	–2.9721	22.057

[1] The best fit.

Growth between sexes

For *M. cephalus*, the growth curves that best fitted observed data were obtained with the Prager method (1987) and Beverton[1] equation (Table 2). In *M. cephalus* females the value of L_∞ is higher than in males, though the differencies between k values are small.

In *M. curema* the growth curves that best fitted observed values were obtained with the Prager (1987) method, as shown in Table 3. The k value in *M. curema* males is higher than in females; therefore males will reach L_∞ faster than females and the growth curve will be slightly more convex. Conversely, the females, showed a slighter growth curve and therefore greater longevity. However, in the case of *M. cephalus*, the k value was observed to be the opposite of that of *M. curema* .

Table 4 contains the values of the parameters and their variances calculated with the Prager method (1987) for both species. The results from the multivariate analysis show that females and males of *M. cephalus* and *M. curema* grow differently (Table 5). The calculated value of T^2 (8928.135) is considerably higher than the tabulated value (11.796, $P<0.01$) for *M. cephalus* and the same happens for *M. curema* , with a calculated T^2 (1843.808) and tabulated value (11.777, $P<0.01$).

Growth in weight

Length-weight relationship The relationships between length and weight stretch to be isometrical (Figs. 3 and 4). In length-weight relationships, dispersion is higher in *M. cephalus* because of the weight of gonads and viscera.

Theoretical growth in weight The theoretical weight for *M. cephalus* and *M. curema* in relation to each age group was obtained employing the mentioned weight equations (Figs. 5 and 6).

Longevity (Age $A_{0.95}$) Both species reach the 95% of L_∞ at the following ages:

Mugil cephalus	*Mugil curema*
$A_{0.95}$ = 28.32 years	$A_{0.95}$ = 18.68 years

The 95% of L_∞ is reached between sexes as follows:

Mugil cephalus	*Mugil curema*
Females = 26.24 years	Females = 19.17 years
Males = 26.46 years	Males = 14.04 years

Discussion

The parameters of the von Bertalanffy growth equation for *M. cephalus* in different areas of the Gulf of Mexico are shown in the Table 6. In the present paper, the value of k, calculated for *M. cephalus* is smaller than values presented by Marquez (1974) and Diaz and Hernandez (1980). Similarly, the values of L_∞ given from these authors are smaller than those obtained in our paper. On the other hand, differences of the growth parameters for the Texas coast (Cech and Wohlschlag, 1975) and Florida (Broadhead, 1958) are very pronounced in relationship to those obtained in our paper: the L_∞ values are smaller.

Table 4

Results of fitting the von Bertalanffy growth equation of females and males of *M. cephalus* and *M. curema*. Entries include parameters estimated and their estimated variance-covariance matrices (S).

Mugil cephalus

Males			Females		
$L_\infty = 603.9$	$k = 0.10536$	$t_0 = -2.979$	$L_\infty = 622.9$	$k = 0.10736$	$t_0 = -2.669$

$$\begin{array}{c} \\ L_\infty \\ k \\ t_0 \end{array} \begin{array}{c} \begin{array}{ccc} L_\infty & k & t_0 \end{array} \\ \begin{bmatrix} 3.1701E{+}02 & -1.1927E{-}01 & -1.3055E{+}00 \\ & 0.4533E{-}04 & 0.5111E{-}03 \\ & & 0.6360E{-}02 \end{bmatrix} \end{array} = S_m \qquad \begin{array}{c} \begin{array}{ccc} L_\infty & k & t_0 \end{array} \\ \begin{bmatrix} 1.8417E{+}02 & -0.5475E{-}01 & -0.5870E{+}00 \\ & 0.1642E{-}04 & 0.1810E{-}03 \\ & & 0.2221E{-}02 \end{bmatrix} \end{array} = S_f$$

Mugil curema

Males			Females		
$L_\infty = 411.8$	$k = 0.1865$	$t_0 = -3.026$	$L_\infty = 454.6$	$k = 0.1355$	$t_0 = -3.94$

$$\begin{array}{c} \\ L_\infty \\ k \\ t_0 \end{array} \begin{array}{c} \begin{array}{ccc} L_\infty & k & t_0 \end{array} \\ \begin{bmatrix} 6.8027E{+}02 & -0.8253E{+}00 & -7.3708E{+}00 \\ & 1.0212E{-}03 & 0.9428E{-}02 \\ & & 0.9296E{-}01 \end{bmatrix} \end{array} = S_m \qquad \begin{array}{c} \begin{array}{ccc} L_\infty & k & t_0 \end{array} \\ \begin{bmatrix} 8.7866E{+}02 & -0.6123E{+}00 & -8.3666E{+}00 \\ & 0.4310E{-}03 & 0.6013E{-}02 \\ & & 0.8794E{-}01 \end{bmatrix} \end{array} = S_f$$

Table 5

Results of the multivariate test between measured growth of males and females from *M. cephalus* and *M. curema*. Entries include the variance–covariance matrix (S) and its inverse (/S), the calculated T^2 statistic, the tabular F and T^2 statistics.

Mugil cephalus

$$\begin{bmatrix} 249.7833 & -0.08662 & -0.94189 \\ & 0.000031 & 0.000344 \\ & & 0.004265 \end{bmatrix} = S \qquad \begin{bmatrix} 0.29749 & 1074.014 & -20.9378 \\ & 4216597 & -102946 \\ & & 3914.545 \end{bmatrix} = /S$$

$$[-50 \quad 0.0097 - 0.12] = [P_m - P_f]'$$

$T^2 = 8928.135^{**}$ $\qquad T^2_{0.01;\,3,\,245} \equiv 11.79551$ $\qquad F_{0.01;\,3,\,245} \equiv 3.9$

Mugil curema

$$\begin{bmatrix} 795.2974 & -0.7018 & -7.94817 \\ & 0.000293 & 0.007448 \\ & & 0.090049 \end{bmatrix} = S \qquad \begin{bmatrix} 0.010014 & -1.37597 & 0.99771 \\ & -2904.87 & 118.8114 \\ & & 89.34055 \end{bmatrix} = /S$$

$$[-42.8 \quad 0.052 \; 0.914] = [P_m - P_f]'$$

$T^2 = 1843.808^{**}$ $\qquad T^2_{0.01;\,3,\,305} \equiv 11.77672$ $\qquad F_{0.01;\,3,\,305} \equiv 3.9$

The values of the parameters of the von Bertalanffy growth equation for *M. cephalus* in different areas are also shown in Table 6. The values of k are higher for the coastal lagoons, whereas the L_∞ values are lower in relation to those obtained for the marine areas; all these differences are important even in areas that are very close (Kesteven, 1942; Thomson, 1951, 1963). Thomson (1951) and Broadhead (1953) found important variations in *M. cephalus* populations in adjacent estuaries; these differences can be explained because of the populational density and abundance of food. On the other hand, Oren (1981) showed that mugilids, because of the accessibility of the lagoons to the sea, can emigrate to the sea at least once per year and mix with other nearby populations. This exodus decreases the amount of local variation in local growth rates.

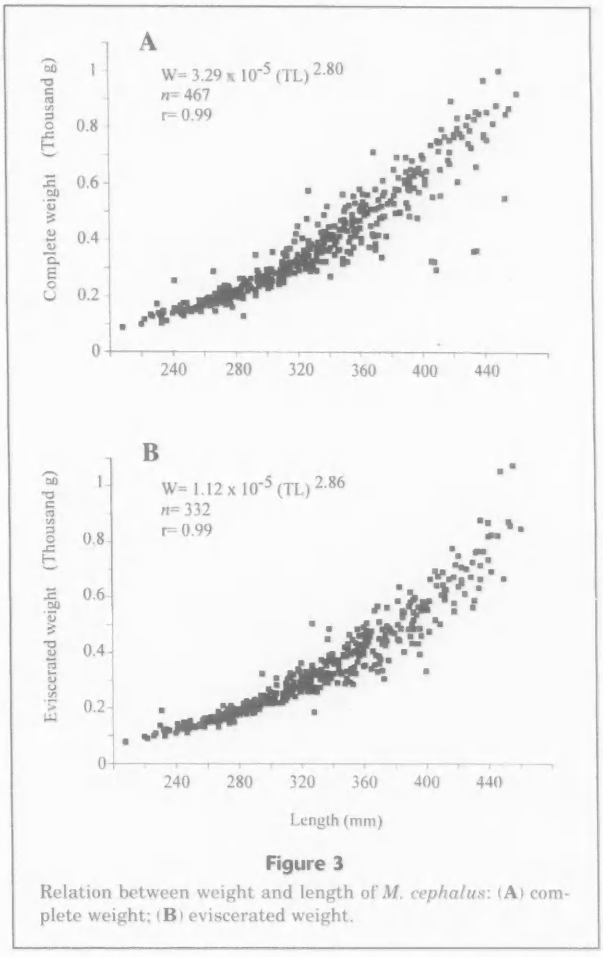

Figure 3

Relation between weight and length of *M. cephalus*: (**A**) complete weight; (**B**) eviscerated weight.

Finally, it is important to take into account that differences between growth rates are important even in areas that are very close; these differences could be explained by the different methods applied for age determination (Oren, 1981); however, these differences could be also explained by the world-wide distribution of this species and its different survival strategies. On the other hand, the differences between growth rates can also occur because of commercial exploitation, for when fishing is very intense, the commercial size of fish decreases and the variations of the k coefficient increase.

The values of the parameters of the von Bertalanffy growth equation for *M. curema* in different areas are shown in Table 7. In our paper, the value of k calculated for *M. curema* shows a higher position in relation to the value proposed by Alvarez (1979) and the value of L_∞ is higher in Cuba. On the other hand, the values of k obtained by Richards and Castagna (1976) in Virginia and by Phillips et al. (1987) in the Nicoya Gulf of Costa Rica show a higher position in relation to the k value obtained in our paper.

For the relation of growth between sexes, some authors have shown that there are no differences between sexes: for *M. cephalus*, Dannevig (1902); Kesteven (1942); Thomson (1951); Morovic (1957); Erman (1959); Thakur (1967); Cech and Wohlschlage (1975); Grant and Spain (1975); for *M. curema*, Alvarez (1979) and Angell (1973). On the other hand, Ezzat (1965), Brulhet (1974; 1975), and Farrugio (1975) have stated that there are differences in the growth between sexes. However, these latter authors did not infer whether these differences in the growth between sexes are significant or not from a statistical point of view. For this reason, a statistical test to compare the growth curves between sexes was

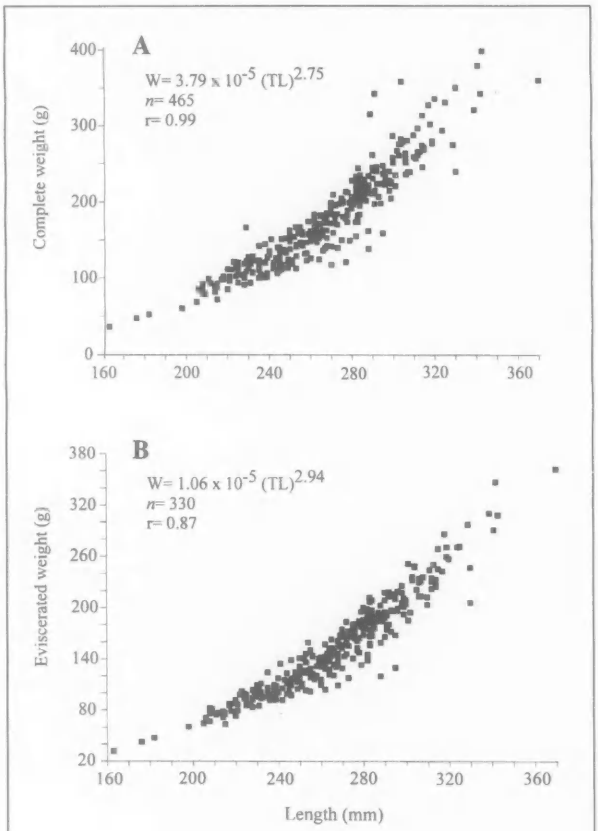

Figure 4

Relation between weight and length of *M. curema*: (A) complete weight; (B) eviscerated weight.

applied in our study (Tables 4 and 5); the results show that there are significant differences in growth between males and females for *M. cephalus* and *M. curema* . Oren (1981) mentioned: "sometimes the females grow slightly faster (Thomson, 1951; Hickling, 1970); Cech and Wohlschlag, 1975), live longer than the males (Thomson, 1951) or at least are predominant among older fish (Hickling, 1970)."

In general, the values of the relationship between length and weight obtained in our study are very similar to those expressed by other authors for coastal lagoons and marine areas. The results obtained for *M. cephalus* are similar to those shown by Kesteven (1942), Morovic (1954), Marquez (1974), Serbetis (1939), and Ezzat (1965). In the same way, the results obtained for *M. curema* are similar to those shown by Angell (1973) and Richards and Castagna (1976).

The longevity values for *M. cephalus* in different localities are given in Table 6. The highest values, 57.6 and 49.9 years, were found in the marine zones by Ilin (1949) in the Black Sea and Kesteven (1942) in Australia, respectively. The lowest values were obtained by Broadhead (1958), 3.7 for males and 4.5 years for females of this species in the marine zones, and by Heldt (1948), 4.6 years in coastal lagoons.

The values of longevity for *M. curema* in different areas are shown in the Table 7. The highest value was obtained by Alvarez (1979), 30 years in Cuba, and the lowest by Richards and Castagna (1976), 3.8 years in Virginia.

The longevity values obtained in the study, 28.3 and 18.7 years for *M. cephalus* and *M. curema,* respectively, showed an intermediate position in relation to the values found by other authors. In all cases, as Taylor (1958) has shown, the longevity and

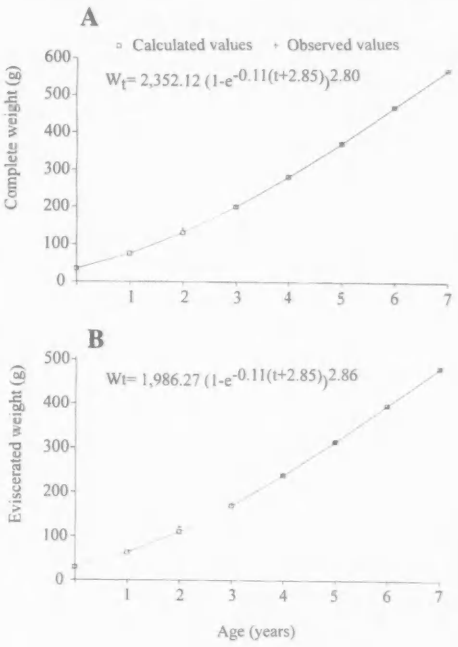

Figure 5

Theoretical growth curve of *M. cephalus*: (A) complete weight; (B) eviscerated weight.

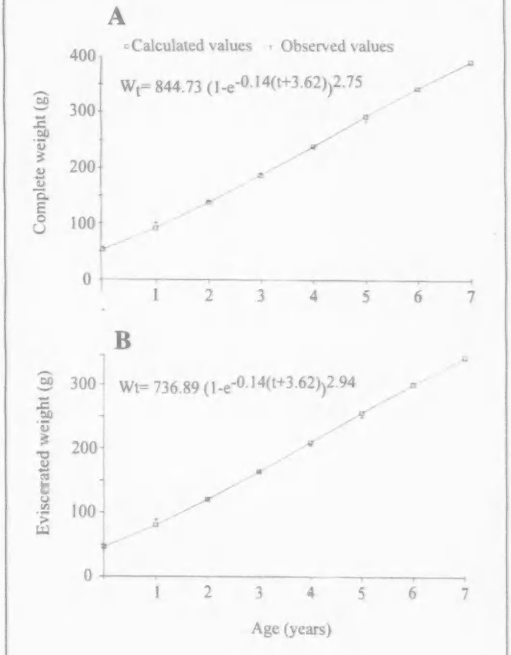

Figure 6

Theoretical growth curve of *M. curema*: (A) complete weight; (B) eviscerated weight.

Table 6

Growth parameters of *M. cephalus* for the Gulf of Mexico and other localities. TL = total length, F = female, M = males, Sp. = species. This table was modified from Tables 5.4 and 5.5 in Oren (1981).

Authority	Locality	Method	Length	Sex	L_∞	k	t_0	$A_{0.95}{}^1$
Gulf of Mexico								
Coastal lagoons								
This study	Tamiahua, Mexico	Otoliths	TL	F	622.9	0.11	−2.670	26.2
		Otoliths	TL	M	603.9	0.11	−2.979	26.5
		Otoliths	TL	Sp.	642.4	0.10	−2.850	28.3
Marquez, 1974	Tamiahua, Mexico	Scales	TL	Sp.	510.0	0.34	−0.114	8.8
Diaz and Hernandez, 1980	Tamaulipas, Mexico	Scales	TL	Sp.	588.0	0.19	−0.213	15.4
Marine zones								
Cech and Wohlschlag, 1975	Texas, USA	Scales	TL	F	407.0	0.32	−0.710	9.4
		Scales	TL	Sp.	450.0	0.24	−0.900	12.5
Broadhead, 1958	N & NW Florida USA	Scales and tag	TL	F	374.0	0.82	−0.160	3.7
		Scales and tag	TL	M	379.0	0.66	−0.036	4.5
Other localities								
Marine zones								
Ilin, 1949	Black Sea	Scales	TL	Sp.	1089.0	0.05	−1.620	57.6
Kesteven, 1942	Australia	Scales	TL	Sp.	1729.0	0.06	−0.510	49.9
Thompson, 1951	West Australia	Scales	TL	Sp.	609.0	0.30	−0.143	10.0
Thompson, 1963	Australia	Scales	TL	Sp.	727.0	0.23	0.006	13.1

continued

Table 6 (continued)

Authority	Locality	Method	Length	Sex	L_∞	k	t_0	$A_{0.95}$[1]
Coastal lagoons								
Romero and Castro, 1983	Chiapas, Mexico	Scales	TL[2]	Sp.	458.5	0.21	–1.770	14.4
Ezzat, 1964	France	Otoliths	TL	Sp.	417.7	0.47	–0.169	6.4
Serbetis, 1939	Rome, Italy	Scales	TL	Sp.	563.0	0.56	0.083	5.3
Morovic, 1954	Venice, Italy	Scales	TL	Sp.	611.0	0.21	–0.465	14.3
Alessio, 1976	Orbetello, Italy	Scales	TL	Sp.	615.0	0.40	–0.044	7.5
Morovic, 1957	Vransko, Yugoslavia	Scales	TL	Sp.	590.0	0.23	–0.083	12.8
Heldt, 1948	Tunisia	Scales	TL	Sp.	620.4	0.65	–0.048	4.6
Farrugio, 1975	Tunisia	Scales	TL	Sp.	693.0	0.19	–0.630	15.8

[1] These values of longevity were obtained in our study by the application of the Taylor method (1958) to the growth parameters given by the authors mentioned in this table.
[2] For the conversion from standard length to TL, the equation given by Thompson et al. (1991) was used.

Table 7
Growth parameters of *M. curema* for other localities.

Authority	Locality	Method	Length	Sex	L_∞	k	t_0	$A_{0.95}$[1]
This study	Tamiahua, Mexico	Otoliths	TL	F	454.6	0.14	–3.900	19.2
		Otoliths	TL	M	411.8	0.19	–3.000	14.0
		Otoliths	TL	Sp.	461.4	0.14	–3.600	18.7
Richards and Castagna, 1976	Virginia, USA	[2]	TL[3]	Sp.	403.4	0.78	–0.060	3.8
Alvarez, 1979	La Habana, Cuba	Spine	TL	Sp.	532.0	0.10	–5.900	30.0
Phillips et al., 1987	Costa Rica	[2]	TL	Sp.	432.0	0.60	–0.244	5.0

[1] These values of longevity were obtained in our study by the application of the Taylor method (1958) to the growth parameters given by the authors mentioned in this table.
[2] = method not indicated.
[3] For the conversion from fork length to TL, the equation given by Thompson et al. (1991) was used.

L_∞ show an inversely proportional relation to the k coefficient.

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Direct observations on the hooking behavior of Pacific halibut, *Hippoglossus stenolepis*

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Abstract.—Direct observation of a 6-hook model setline off Canada's northwest coast with an underwater camera allowed estimation of approach direction, attack rate, and hooking success for Pacific halibut (*Hippoglossus stenolepis*). In observations of 129 halibut approaches, 29 halibut simply continued swimming past the gear and away. The remaining 100 halibut responded in some way to the gear, exhibiting behaviors ranging from a simple change in swimming direction toward the gear, to bites on the baited hooks. Behavior transitions are described both leading up to and following 57 observed bites. Halibut displayed a positive rheotactic response; 74% approached upstream toward the bait. A higher proportion of upstream approaches resulted in bites than approaches from other directions or approaches that occurred during slack current. Most bites were associated with a vigorous rushing behavior, which often led to hooking. Hooking success was demonstrated to be length-dependent, ranging from zero for the smallest fish to approaching one for the largest sizes caught. Very low rates of hooking success were observed for some rockfish, which in some areas are important bycatch species of the halibut fishery.

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The International Pacific Halibut Commission (IPHC) sets harvest quotas for the stock of Pacific halibut (*Hippoglossus stenolepis*) off the Pacific shores of the United States and Canada. An important tool in setting these quotas is the catch per unit of effort (CPUE) both of the directed commercial fisheries of these countries and of setline surveys conducted annually by the IPHC. The trends in these CPUE indexes, both among areas and over years, are important to the IPHC stock-assessment model. Over the years, the IPHC has conducted fishing experiments in order to understand different aspects of CPUE. A selection curve for the size 16/0 J-style hooks used in the fishery prior to 1984, demonstrated by Myhre (1969), ranged from zero for fish around 40 cm, to one for fish around 80 cm. The mechanism for size selection in halibut has not been demonstrated. Skud (1978) reported that halibut was a dominant predator, probably more successful than other species in competing for setline baits, and concluded that although other fish and invertebrates, even if not caught, could cause bait loss, competition by these species was unlikely to affect the CPUE of halibut. Later studies with circle hooks (Hoag et al., 1984; Kaimmer and St-Pierre, 1993) demonstrated effective competition by a decreased catchability of halibut associated with the presence of large numbers of spiny dogfish (*Squalus acanthias*).

Attack rate (bites/fish) and hooking success (hookings/bite) by fish length are important parameters of most hook-catch models (Deriso and Parma, 1987), although these parameters often must be estimated from either a theoretical model or observations of captive fish. This paper presents results from an IPHC study designed to estimate these parameters directly from observations of halibut approaches and of bites on the circle hooks used in the present-day fishery. These behavioral studies conducted in the field, rather than through observation of captive fish, should yield results most applicable to and representative of setline catches of wild fish (Løkkeborg et al., 1993).

Materials and methods

Vessel and area

A 12-day experiment was conducted 11–20 June 1994 from a 15.5-m chartered vessel. An underwater camera permitted a view of a model setline consisting of six baited fishing hooks. The gear was placed at various halibut habitats in the Queen Charlotte Islands of British Columbia, Canada. This region was chosen to provide an opportunity to view a variety of halibut habitats, in terms of depth and bottom type, with a likelihood of relatively good water clarity. The midsummer timing allowed for the presence of halibut on their midyear feeding grounds, long working days, the opportunity of fair weather, and a window between expected plankton

blooms. Camera equipment was deployed 45 times, primarily off the northern and northwestern shores of the Queen Charlotte Islands (Fig. 1). Bottom habitat ranged from mud or soft sediment, gravel, cobbles, or large boulders, to steep ledges. Deployments were intended to last about one hour. Problems with strong currents or the loss of four or more baits due to fish captures or other reasons resulted in early gear retrievals. Longer deployments resulted from gear retrieval problems. Time on bottom for each deployment averaged 58 min (range 14–150 min, SD 28 min). Average depth for all sets was 67 m (range 11–84 m).

Equipment

A silicone-intensified tube (SIT) monochrome video camera (model OE1323, Osprey Electronics Ltd., Aberdeen, Scotland) was housed in an enclosure featuring both pan and tilt functions. This enclosure was mounted in an aluminum cage connected by 5-cm aluminum pipe to a square base frame constructed of 5-cm steel pipe (Fig. 2). The camera–frame assembly was deployed by, and monitored through, an electromechanical cable. All observations were made by using ambient available light.

A 0.8-cm (5/16-inch) diameter groundline was suspended about 30 cm inside the base frame by short lengths of elastic cord attached to the inside corners of the steel frame. This arrangement resulted in an elastic attachment for the hooks and gangions. This "soft" attachment was probably a more realistic model of the behavior of a gangion on a groundline than an attachment made directly to the rigid steel frame. The study used 16/0 circle hooks (O. Mustad and Sons, Oslo, Norway, Quality 39965), the size and style most commonly used in the Pacific halibut fishery, and the standard in IPHC surveys. Hooks were attached by 81-cm (32-inch) gangions and snaps to the suspended groundline, one per side alternating with two per adjacent side, for a total of six hooks. All hooks were baited with 0.17-kg (1/3-lb) pieces of chum salmon (*Oncorhynchus keta*) fillet with skin intact.

Observation of a 25-cm length of flexible surveyor's tape attached to one of the aluminum legs, as well as of dust or sediment plumes during bait attacks, was used to determine the direction of bottom current and also as a qualitative measure of current strength. The video signal was monitored and recorded at all times. When viewed directly from above, all parts of the square base were within the field of view. This usually meant that all six hooks could be viewed at the same time. When one or more hooks lay outside the base frame, the camera was periodically redirected for viewing these outside hooks.

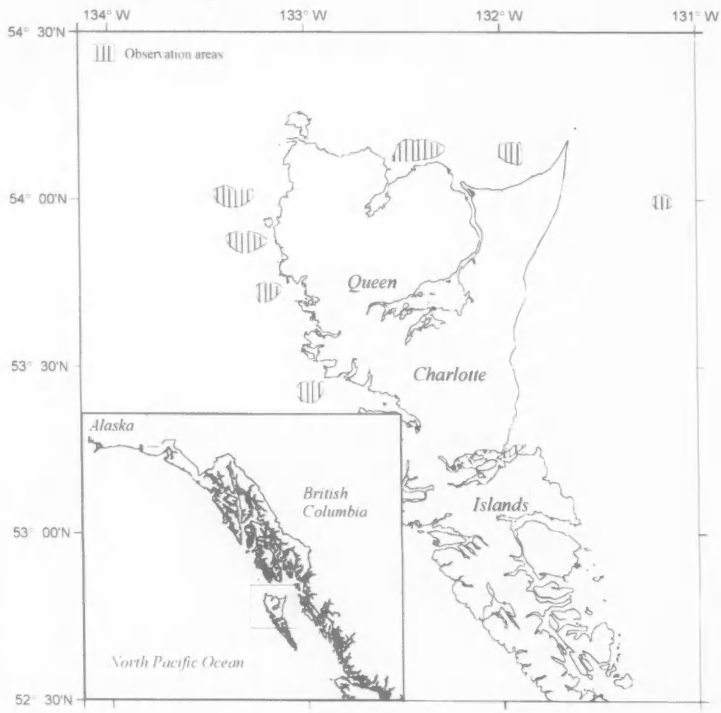

Figure 1

Location of camera deployments. Box in inset shows general area of operation.

Fish length and distance measurements

Lengths of 20 hooked and landed halibut were measured. During video editing, relative fork lengths for all halibut that could be clearly viewed on or near the bottom and at or near the center of the frame were obtained by using a vernier caliper held against the video screen while the video image was frozen. The linear regression between measured and relative fork length (r= 0.74) was used to estimate the fork lengths of 92 fish not captured and retrieved, as well as the distance from fish lying on the bottom to the nearest baited hooks. Caught fish, other than halibut, were weighed to the nearest 0.5 kg on a spring scale.

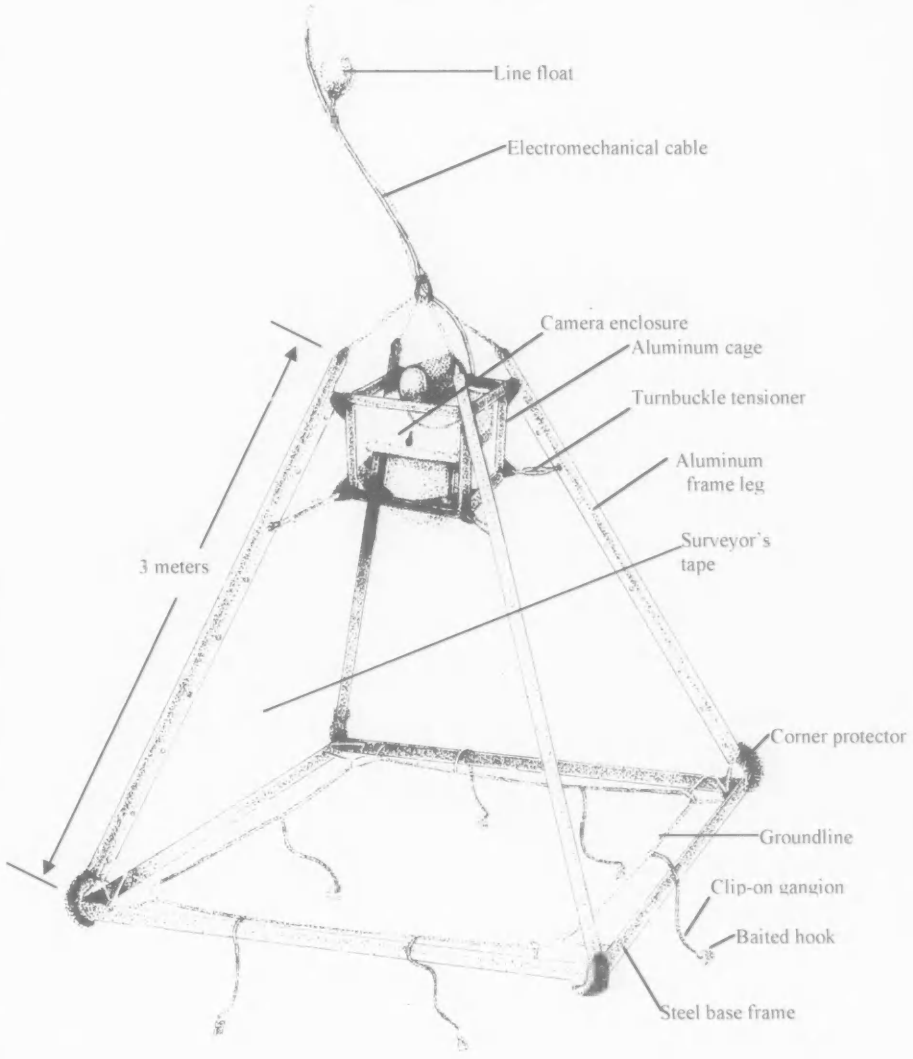

Figure 2
Camera cage and frame, showing attachment of groundline and baited hooks.

Observations of behavior

Appearance and subsequent behavior sequences were recorded for all halibut, including the directions of both appearance and departure in relation to the bottom current. All behaviors were coded as to time at which the behavior either occurred or was initiated, to the nearest second. Behavior codes were modified from those used by Fernö et al. (1986). For species other than halibut, only bites and hookings were recorded. Unless otherwise specified, code descriptions and frequencies refer to halibut only.

Behavior definitions

The word "observed" was recorded upon the first appearance of a halibut, along with its approach direction in relation to the bottom current, and a number was assigned to the fish in order to identify future observations on that fish.

The word "looping" was recorded when a swimming fish made a turn of more than 90 degrees.

"Lying" was recorded when a fish stopped swimming and lay on the bottom, and included (for fish that lay near hooks) direction to the closest baited hook in relation to bottom current.

"Biting" was recorded when a fish took a baited hook completely into its mouth.

An "incomplete biting" was recorded when a fish touched a bait but the bait or hook was never completely within its mouth.

"Grazing" was recorded if a fish bit at a piece of bait that was not attached to a hook. Pieces of bait would occasionally fall free from the hook during the rushing following a bite.

"Rushing" was recorded when a fish swam rapidly forward with the bait or hook in its mouth.

"Spitting" was recorded when bait was either spat or pulled out of a fish's mouth.

"Hooking" was recorded when a fish retained a hook in its mouth for at least twenty seconds, usually while the fish struggled or fought violently. This time period was chosen as consistent with that in other literature on hooking behavior (Fernö et al., 1986; Huse and Fernö, 1990). However, hooking was not recorded until completion of the rushing behavior. When biting was followed by rushing lasting more than twenty seconds, which was in turn followed by spitting, that portion of the behavior sequence was listed as "biting, rushing, spitting." A fish that rested after rushing with the hook still in its mouth, and which subsequently after twenty seconds or more rushed and spat out the hook, was listed as "biting, rushing, hooking, lying, rushing, spitting."

"Attacking" was recorded when a fish chased or bit at another fish, either a halibut or one of the other species in the viewing area.

"Departure" was recorded, along with direction of travel in relation to bottom current, when a fish left the observation area. Occasionally, a fish would leave the observation area and be identified on its subsequent return by a short duration of absence (less than 5 s), and by its length, and body markings. In these cases, the period of nonobservation was recorded as "looping."

Sequential occurrences of either lying or looping were coded as single occurrences. Consecutive lying behaviors were coded as a single behavior occurrence only when the subsequent lying was the result of a small position shift and the fish did not shift to a different bait. Twenty-one occurrences of behaviors were considered compromised by the experimental setup. A behavior transition beginning with a compromised behavior was considered invalid. For example, a bite where the hook or gangion was wrapped around the frame was considered compromised, and the transition to the following behavior was considered invalid.

Direction in relation to bottom current

Fish approaching or departing within 67.5° to either side of and into the current were coded as "upstream." Fish swimming within the next 45° on either side of the current (within a 22.5° arc to a line perpendicular to the current) were coded as "right angle to the current." Fish swimming within 67.5° to either side of and out from the current were coded as "downstream." These same criteria were used to record the direction in which a fish was lying in relation to a bait.

Results

The number of halibut observed was 129, ranging from none (on 19 sets) to a high of 19 (on one set). On average, 5.6 halibut were observed on sets where at least one halibut was seen, and the numbers of halibut caught per set ranged from 0 to 4. Measured fish ranged from 72 to 114 cm in length (mean=86.8 cm, SD=11.4 cm). Calculated lengths ranged from 52 to 196 cm (mean=90.1 cm, SD=24.2 cm).

Behaviors and behavioral transitions

The time until first appearance of the first halibut in a set varied widely, ranging from almost immediately (18 s) to more than an hour after the gear was set (1 h 1 min), and averaged 18 minutes (SD=13 min 32 s). For 29 fish that swam away immediately after observation, the time between appearance and departure ranged from 7 to 33 seconds (mean=9 s, SD=7 s). Orientation in relation to bottom current was noted for 93 halibut approaches (Fig. 3). Another 18 approaches were noted as occurring during slack current. Of those fish that approached during periods of noticeable current, 75% approached upstream, 9% approached at right angles to the current, and 17% approached downstream.

Looping and lying were the most common behaviors, with 80 loopings recorded for 60 halibut and 70 lyings recorded for 45 halibut (Table 1). The average durations of looping and lying behaviors were 40 and 14 seconds, respectively (Table 2). Fifty-seven bites were observed; 48 halibut made a single bite, 3 halibut made 2 bites, and 1 halibut made 3 bites. A total of 25 halibut were classed as hooked. The transition matrix in Table 3 details 426 valid behavior transitions constructed from the observations. The main

function of the matrix was to show possible patterns or combinations of behaviors that occurred more or less frequently than expected if all possible behavior transitions had the same probability of occurring. Statistical analysis of this matrix is complicated by the fact that not all transitions were possible (a spitting may only follow after biting or rushing). The matrix was therefore visually inspected for large differences, as recommended by Slater (1973).

Prebiting behavior and attack rate

There were 293 transitions observed for halibut, not including behaviors that followed initial complete bitings. The number of prebiting transitions per individual fish ranged from one to fifteen, with 78% of the fish making three or less transitions, and over 90% making five or less.

Looping and lying near bait were the most common behaviors following initial observation. Less commonly observed were departures, biting, and incomplete biting. Looping behavior was followed about equally by lying near bait, biting, and departure. Lying near bait was most often followed by either looping or biting, and less often by departure or an incomplete biting. For 71 occurrences of lying behavior, 8 either had no obvious hook orientation or occurred during slack current, 3 fish lay upstream of bait, 26 lay to the side of bait, and 34 lay downstream from bait. The distance from bait for fish lying beside or downcurrent averaged 13.2 cm (SD=8.4 cm) and 14.6 cm (SD=9.0 cm), respectively. Incomplete biting was most often followed by lying near bait, and less often by departing or looping.

The transitions in Table 3 do not consider preceding behaviors, or how many previous behaviors a particular fish had completed. As each of the original 129 halibut was observed through the first four behavior transitions up to either biting or departing, there was a tendency for fish to stay in interaction with baits. Lying, incomplete and complete biting, and grazing are all behaviors that are direct interactions with either the bait or food present around a baited hook. In the first transition (n=129), fish were most likely to interact with bait (43%), loop (34%), or depart (23%). About one-third of the bait interactions in the first transition were bites. In the second transition (n=78), fish were most likely to interact with the bait (57%) or depart (40%). Only 12% looped. Again, about one-third of the bait interactions were bites. By the third transition (n=28), fish were much more likely to continue bait interactions (68%) than they were to loop (25%) or depart (7%). About one-quarter of bait interactions were bitings.

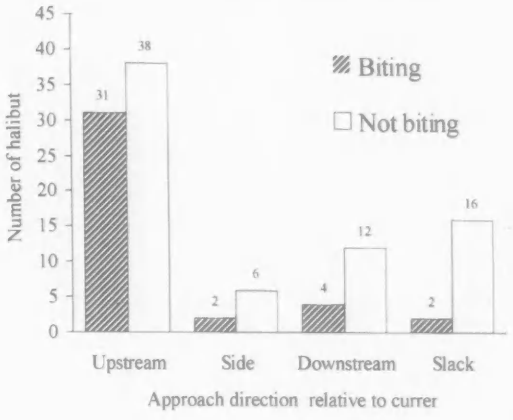

Figure 3

Numbers of halibut biting and not biting, by approach direction in relation to bottom current.

Table 1

Frequencies of halibut behaviors observed. Individual fish may be counted as performing more than one behavior.

Behavior	Count	Number of individual fish
Appearance	129	
Looping	80	60
Lying	70	45
Incomplete biting	15	9
Biting	57	52
Rushing	53	48
Hooking	25	25
Spitting	30	27
Grazing	4	3
Attacking	3	3
Departure	96	—
Grand total	562	

In the fourth transition (n=21), 62% continued with bait interactions, almost half of which were bitings, 21% departures, and 19% loopings. By the end of the fourth behavior transition, out of the original 129 halibut observed, approximately half (66 fish) had departed, whereas just over a third (47) had made complete bites. In each of the transition levels, 43–68% of behaviors were directed toward baits.

Elapsed time between appearance and the first observed bite for all halibut ranged from 1 s to 7 min 54 s (mean=34 s, SD=1 min 5 s). Ninety-five percent

of first bites occurred in less than 1 min 20 s after first appearance, and 50% occurred within the first 20 s. Although no significant difference was noted between time to first bite and approach direction, for the 36 observations where the approach was made during some current, the maximum time to first bite was 2 min 51 s. Of two bites following appearances during slack current, one bite occurred almost 8 min

Table 2

Duration of observed halibut behaviors.

Behavior	No. of observations	Duration	
		Range	Average (±SD)
Prior to hooking			
Looping	80	3 s–6 min 32 s	40 s (±62 s)
Lying (prior to hooking)	70	1–68 s	14 s (±15 s)
Rushing (followed by spitting)	31	1–63 s	10 s (±13 s)
Rushing (followed by hooking)	22	24 s–3 min 30 s	86 s (±44 s)
Following hooking			
Lying	34	3 s–22 min 8 s	3 min 49 s (±5 min 19 s)
Rushing	24	8–78 s	31 s (±19 s)

Table 3

Transition matrix of observed values (upper number) and expected values (in parentheses) for the frequency of transitions from one behavior to another within behavior sequences. Top row is the first behavior in a transition and the leftmost column is the second behavior. For example, a fish that was observed, made one loop, and then swam away would have two tallies in this table, one for "appearance" followed by "looping," and a second for "looping" followed by "departure." Behavior transitions starting with compromised behaviors are not included in this table.

	First behavior									
Second behavior	Appearance	Looping	Lying	Incomplete biting	Grazing	Biting	Rushing	Spitting	Attacking	Total
Departure	29 (38.0)	30 (28.7)	12 (25.3)	3 (3.8)	— (0.9)	—	—	20 (8.8)	— (0.6)	94
Looping	44 (31.1)	—	21 (20.7)	2 (3.1)	— (0.7)	—	—	9 (7.2)	1 (0.5)	77
Lying	32 (28.3)	27 (21.4)	—	8 (2.8)	2 (0.7)	—	—	— (6.6)	1 (0.4)	70
Incomplete biting	4 (6.1)	1 (4.6)	10 (4.0)	— (0.6)	— (0.1)	—	—	— (1.4)	— (0.1)	15
Grazing	— (1.6)	1 (1.2)	3 (1.1)	— (0.2)	— (0.0)	—	—	— (0.4)	— (0.0)	4
Biting	19 (23.1)	15 (17.4)	21 (15.3)	1 (2.3)	— (0.5)	—	—	1 (5.4)	— (0.4)	57
Rushing	—	—	—	1 (2.1)	—	52 (27.2)	—	—	—	53
Spitting	—	—	—	—	—	2 (14.9)	27 (27.4)	—	—	29
Hooking	—	—	—	—	—	1 (12.9)	24 (23.6)	—	—	25
Attacking	1 (0.8)	— (0.6)	— (0.5)	— (0.1)	1 (0.0)	—	—	— (0.2)	— (0.0)	2
Total	129	74	67	15	3	55	51	30	2	426

after initial appearance, more than twice the longest elapsed time between appearance and first bite for fish that appeared when bottom current was noticeable.

There were differences in the biting behavior of halibut associated with their direction of approach in relation to bottom current (Fig. 3). The difference was significant (upstream 45%, side or downstream 25%; χ^2=33.1, P<0.0125), as was the difference between fish that approached when current was or was not noticeable (current 49%, no current 11%; χ^2=5.4, P<0.0125). Overall, attack rate (bites/fish) was 33–73% over the range of lengths observed (Table 4). Although approach direction in relation to current had a significant effect on attack rate, there was no relation between fish length and attack rate for 41 halibut that had approached upstream. For these fish, the attack rate for fish less than 82 cm (sublegal size) was 46% (11 of 24), and the rate for fish 82 cm or larger (legal size) was 47% (8 of 17).

Direction in relation to the current was noted for 54 departures. Thirty-three (61%) halibut departed upstream, 6 (11%) departed at right angles to the current, and 15 (26%) departed downstream.

Postbiting behavior and hooking success

Almost all bites (95%) occurred while fish were in motion: a fish swam toward the bait, took the bait in its mouth, and continued swimming (rushing). In two cases, a lying fish took bait and subsequently spat it out without rushing. In one case, a lying fish kept the bait in its mouth long enough (20 s) to be classified as hooked, but without rushing.

Rushing behavior was about equally followed in frequency by either spitting the hook (53%) or hooking (47%). On average, spitting occurred 10 s after the start of rushing behavior; rushing that did not result in spitting had an average duration of 86 s (Table 2). In two-thirds of the cases where the hook was spat, the fish departed rapidly. Thirty percent of spittings were followed by looping behavior and, in one case, the fish immediately rebit the hook. One "steal" was observed, where the fish swam free from the hook with the entire bait in its mouth. Hooking success (hookings/bite) by 5-cm length group was 0–83% and increased steadily with increasing fish size. The difference in hooking success between fish of sublegal (<82 cm) and legal (≥82 cm) length was highly significant (38% vs. 71%; χ^2=4.36, df=1, P<0.025).

Figure 4 shows observed postbiting behavior transitions, from an initial complete bite by an individual fish through the fourth behavioral transition. Of 50 fish tracked on this chart, 20 ended up departing, 22 ended up hooked, and 3 were still interacting with hooks at the end of the fourth behavioral transition. Of the three continuing interactions, one fish lay near bait and two fish rebit baited hooks. Fifty percent of

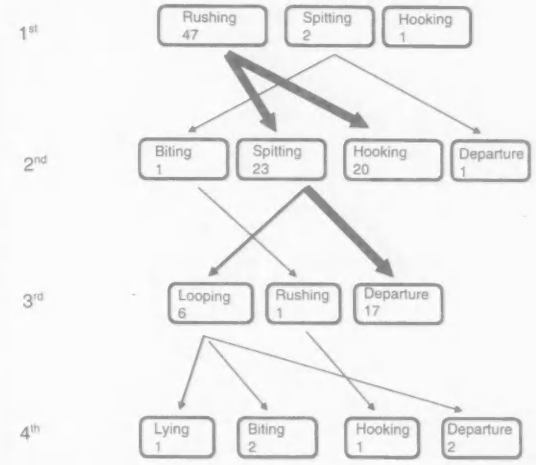

Figure 4

Behavior tree describing behavior sequences following an initial complete bite. Numbers at left of rows are the position of behaviors in sequences following initial observation. Numbers in boxes are the total frequencies of each behavior in a row position. Thickness of arrows represents relative numbers of observations for each behavior transition. Because some behaviors were compromised, not all behaviors have transitions from one row position to the next.

Table 4

Halibut attack rate (% of fish biting) and hooking success (% of bites resulting in hooked fish) by 5-cm group.

Size class (cm)	Number observed	Number of bites	% bites	Number hooked	% hooked
62–67	6	3	50	0	0
68–72	11	5	45	1	20
73–77	17	9[1]	53	3	38
78–82	11	8	73	5	63
83–87	12	5	42	3	60
88–92	18	6	33	4	67
93–97	12	6	50	5	83
Total	87	42		21	

[1] One bite in the 73–77 cm size class was compromised. Percentage hooked is determined from the eight uncompromised bites.

spits occurred in less than 5 seconds, and 95% occurred in less than 25 seconds. Once hooked, and after initial rushing, the halibut lay on the bottom, resting, then went into a pattern of rushing, resting, rushing, etc. There appeared to be a pattern of decreasing duration of rushing following subsequent rest periods. The average times for resting and rushing after the initial hooking were 3 min 49 s, and 31 s, respectively (Table 2).

Hooking success for other species

The range of approach and interaction behaviors for species other than halibut was not documented beyond noting bitings and subsequent hooking. Other species that bit at hooks included canary rockfish (*Sebastes pinniger*), yelloweye rockfish (*S. ruberrimus*), quillback rockfish (*S. maliger*), ratfish (*Hydrolagus colliei*), and lingcod (*Ophiodon elongatus*). In general, hooking success for the major rockfish species was around 5–6% (Table 5). These fish were comparable in average size (weight) to those caught as incidental catch in the directed halibut fishery.

Discussion

The feeding behavior of halibut may be classified into three phases: arousal, search, and bait attack and food ingestion.

Arousal

In most cases, arousal to the presence of food occurs at a distance, and bait odor carried by bottom currents attracts fish from well beyond the limited viewing distance of the present experiment. Although undoubtedly involving detection of an odor plume (Atema, 1980), the present experiment did not investigate the initial arousal phase of feeding behavior.

Table 5

Hooking success for species other than halibut.

Species	Number of bites	Number hooked	% hooked	Average weight (kg) of hooked fish
Canary rockfish	339	17	5	4.0
Yelloweye rockfish	237	20	8	3.8
Quillback rockfish	228	9	4	1.9
Ratfish	36	1	3	N/A
Lingcod	23	9	39	11.1

However, a number of observations in relation to food location and uptake were made.

Search

It is clear that halibut use orientation to bottom current to locate food, most approaching upstream when a bottom current was present. This rheotactic orientation is used by many fish for detection and location of prey (Atema, 1980; Løkkeborg et al., 1989; Løkkeborg, 1998). Once fish are aroused to the presence of a prey item by scent, they orient into a current to locate the food.

The role of vision in food location by Pacific halibut was less clear. Behaviors directed towards the gear were observed in some cases immediately after the gear reached the seafloor. These were likely responses to visual clues. However, the greatest number of appearances appeared to be motivated by scent carried by the current. Although earlier studies have shown that halibut certainly prey on a number of pelagic or semipelagic species where vision must play an important role in prey recognition and capture (Best and St-Pierre, 1986), it probably played a limited role in behavior toward the model setline.

Prebiting behavior and attack rate

Fish vary widely in their reliance on sight, smell, and touch in deciding whether to accept or reject food once it has been located (Løkkeborg, 1994). Both looping and lying behaviors were common in the observed halibut, and in only a few cases was a complete bite initiated without some preliminary bait interaction such as looping or lying. Looping behavior could be a test of an odor plume by the fish, assuring that the fish is in an area of high-scent concentration. Many halibut lay near the bait prior to initiating a bait attack, most either directly downstream or to one side of the bait in relation to the current. This behavioral response may reinforce olfactory clues that led the fish to the bait, or possibly a restrained response to the baited hook as a novel prey item (Løkkeborg, 1990). Rejection of the bait at this point was often followed by looping, behavior that often led to further bait interaction. The role of mechanoreception was not demonstrated. In only a few instances did halibut exhibit incomplete bites, and these generally did not result in the fish then leaving the area of the gear. Most bites were associated with extremely active behavior, e.g. a fish beginning to rush simultaneously with biting the bait. Only one bite that resulted in hooking was not followed by a rush.

In the simplest interpretation, the attack rate for halibut was 43%. Fish length was not a significant

factor in attack rate, although approach direction was highly significant; fish that approached the bait upstream bit almost twice as often as fish that approached from the side or downstream, and four times as often as fish that approached during slack current. It is likely that fish approaching upstream were following a scent trail from the baits and had a higher motivation to bite than fish that approached from other directions.

It is interesting to note that although halibut appeared throughout the gear deployment, consistent with the idea of being aroused by and following a scent plume from different distances, once a fish arrived at the area of the baited hooks, bait attacks occurred quickly. Most attacks occurred within the first minute after a halibut appeared, and less than five percent of the bait attacks occurred more than one and one-half minutes after the fish appeared.

Postbiting behavior and hooking success

In almost all cases, complete bites were followed by rushing behavior, which resulted in about equal numbers of hooked fish and fishes that spat the hook and then departed the observation area. Hooked fish struggled violently for a short period, then went into a series of resting and rushing behaviors which continued through the observation period, the duration of rushes becoming gradually shorter.

Size selectivity by hook-and-line gear has a number of components, including encounter rate, attack rate, and hooking success. A higher encounter rate has been shown for larger fish, which may have greater foraging ranges and therefore a higher probability of encountering baited gear (Løkkeborg and Bjordal, 1992; Engås and Løkkeborg, 1994; Bjordal and Løkkeborg, 1996). It is possible that the present experimental arrangement was skewed in this way toward catching larger halibut. Attack rate has been related to bait size for some species; larger fish show a preference, and therefore a higher attack rate, for larger baits, and smaller fish showing a preference for smaller baits (Bjordal and Løkkeborg, 1996). No difference in attack rate by fish size was seen in the present study.

Hooking success was found to be strongly dependent on fish length, ranging from zero for fish less than 62 cm, to 83% for fish 93–97 cm (Fig. 5). This finding is consistent with and can explain much of the selectivity estimated from representative IPHC commercial and setline survey data (Clark[1]). A circle hook is designed so that it is pulled to the corner of the mouth during rushing, with the point of the barb in line with the pull of the gangion (Bjordal and Løkkeborg, 1996). Hooking results from the orientation of the hook during the rush and the penetration of the barb caused by the pull on the gangion during that rush, the point of the hook circling the jawbone and exiting through the cheek (Johannes, 1981). Ninety to ninety-five percent of halibut caught on circle hooks are hooked in this manner (Kaimmer and Trumble, 1997).

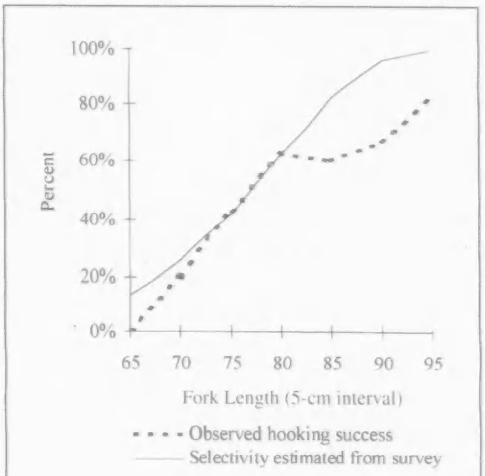

Figure 5

Hooking success from direct observation and selectivity estimated from IPHC survey data by 5-cm length groups.

Hooking success has been related to hook size only when the range of hook sizes is very great, on the order of 200% or more (Løkkeborg and Bjordal, 1992) and has been explained in terms of larger fish being able to exert a stronger pull on the gangion during rushing. This stronger pull generates the greater force necessary to pull the point of a larger hook fully into the tissue of the mouth cavity, resulting in a higher rate of hooking success. A greater hooking success as the result of a larger fish exerting a stronger pull may be countered by weaker tissue in the mouth of smaller fish, requiring less force for the hook to penetrate (Bjordal and Løkkeborg, 1996). The hooking success table (Table 4) in this study was constructed for fish 62–97 cm in length, the largest just 1.5 times the length of the smallest, and showed dramatic differences in hooking success over length changes as small as 10–20 cm. Some mechanism beyond pull strength was probably responsible for these differences. In an earlier study where the same hooks

[1] Clark, W. 1997. Coastwide distribution of exploitable biomass according to 1997 setline surveys. Int. Pac. Halibut Comm. Rep. of Assessment and Research Activities, p. 161–202. International Pacific Halibut Commission, P.O. Box 95009, Seattle, WA 98105-2009. Unpubl. manuscript.

(Kaimmer, 1994) were used, halibut less than 82 cm in length were hooked more often in locations other than the jaw than were larger halibut. Although this difference was small, it suggests a functional relation between the mechanical operation of the hook and the size of the fish's mouth in relation to overall hook and bait dimensions. A higher rate of hooking success for smaller halibut might have been seen if smaller bait had been used. This was not tested in the present experiment because bait size was held constant to the standard used in IPHC setline surveys and representative of the commercial halibut fishery.

It is clear that an increased hooking success for larger fish has a dramatic effect on the size selection of longline gear. Much of the length-based selectivity assumed for halibut setlines can be explained by the differences in hooking success by fish length demonstrated by this study. The selection curve generated from the present observations is the first to be determined for Pacific halibut through direct observation of hook attacks.

Conclusions

We consider the results of this study to be qualitative, not quantitative. Their application to commercial or experimental longline sets or CPUE indices should take into account the limited nature of the experiment, both in terms of number of hooks fished and in terms of lack of seasonal or wide areal variation in the observations. Although it is likely that the results are generally applicable to halibut, they could vary significantly for fish with different feeding histories in a different life stage. Attack rate particularly could be susceptible to the condition of fish in relation to recent feeding or spawning activity. The primary objective of this project was to determine estimates for the attack rate and hooking success of Pacific halibut on gear typical of those used in the commercial fishery. Results show that although these parameters may be estimated, their values are influenced by a number of factors, most notably by the presence of bottom current and direction of approach in relation to that current (for attack rate) and fish length (for hooking success). The behavioral sequences observed for Pacific halibut were fairly limited and included searching into a current for food, looping and lying around or near bait items, and a vigorous biting–rushing sequence that often resulted in hooking. The relative absence of physical contact with the bait prior to biting (such as tasting) might indicate that texture is less important for food selection by halibut. The role of vision in halibut feeding was not tested.

The large number of bait attacks by species other than halibut compensated for the very low hooking success for these species. In fact, we caught more of these species than halibut during the experiment. Although their presence or interaction with baits short of hooking did not seem to affect the attack rate of halibut that were present, the removal of available baits by interspecies competition should be included in any model of hook-and-line CPUE.

Acknowledgments

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Mitochondrial DNA analysis of population structure in the Atlantic croaker, *Micropogonias undulatus* (Perciformes: Sciaenidae)

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Abstract.—Genetic population structure in Atlantic croaker (*Micropogonias undulatus* Linnaeus) was examined by using the polymerase chain reaction (PCR) and restriction fragment length polymorphism (RFLP) analysis of mitochondrial DNA (mtDNA). Juvenile croaker from three U.S. Atlantic localities (Delaware, North Carolina, and Florida) and one Gulf of Mexico locality (Louisiana) were screened to document the magnitude and spatial distribution of mtDNA variation in *M. undulatus*; to evaluate the integrity of Cape Hatteras, North Carolina, as a genetic stock boundary; and to estimate levels of gene flow among Atlantic localities to provide an improved basis for future decisions regarding coastwide management of this fishery resource.

RFLP analysis of the ATPase 6 and D-loop mtDNA regions revealed a total of 15 composite haplotypes in 93 individuals. Monte Carlo simulations revealed no geographic heterogeneity in mtDNA haplotype frequencies among Atlantic localities and no evidence that juveniles collected north and south of Cape Hatteras originated from separate gene pools (net sequence divergence=–0.002%). There was significant heterogeneity between Atlantic and Gulf of Mexico samples, suggesting restricted gene flow between these two regions. Analysis of molecular variance also indicated regional (Atlantic versus Gulf) population structure, but provided no evidence that Cape Hatteras represents a genetic stock boundary. AMOVA indicated relatively high gene flow (N_fm = 12–23 effective female migrants per generation) among Atlantic localities. These findings are consistent with 1) a single genetic stock of *M. undulatus* on the Atlantic coast and 2) separate, weakly differentiated stocks in the Atlantic and Gulf of Mexico.

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Atlantic croaker (*Micropogonias undulatus* Linnaeus) is an important commercial and recreational fishery species along the U.S. Atlantic and Gulf of Mexico coasts (Chao and Musick, 1977; Mercer[1]). On the Atlantic coast, *M. undulatus* is common in estuarine and coastal waters from Indian River, Florida, to Chesapeake Bay (Nelson et al., 1991; Stone et al., 1994). Current fishery management practices for *M. undulatus* assume a single or "unit" stock for the entire Atlantic coast (Kline and Speir, 1993) despite indications that two stocks may exist. The two-stock hypothesis is based on variation in life history traits and population dynamics of Atlantic croaker occurring north and south of Cape Hatteras, North Carolina. White and Chittenden (1977) reported lower mortality rates, greater longevity, and larger maximum size for *M. undulatus* north of Cape Hatteras. Ross (1988) concluded that two groups with contrasting life histories may overlap in the vicinity of Cape Hatteras, with the northern, mainly offshore group exhibiting greater size-at-age, greater longevity, lower annual mortality, and delayed maturation compared with southern individuals. Geographic variation in biological characteristics of northern and southern *M. undulatus* implies that these groups may respond independently to exploitation and may require management as separate stocks; however, the basis for these differences (i.e. genetic or ecophenotypic) is unclear.

Identification of Atlantic croaker stock structure was listed among the priority research needs by the 1981 Sciaenid Assessment Workshop sponsored by the Atlantic States Marine Fisheries Commission (ASMFC) and National Marine Fisheries Service (Wilk and Austin, 1981). The Atlantic Croaker Fishery Management Plan, prepared under the ASMFC Interstate Fishery Management Program, also recommended research to identify croaker stocks along the Atlantic coast (Mercer[1]). In the present study, polymerase chain reaction (PCR) and restriction fragment length polymorphism analysis

[1] Mercer, L. P. 1987. Fishery management plan for Atlantic croaker. Fisheries Management Rep. 10, Atlantic States Marine Fisheries Commission, Washington, D.C., 90 p.

Table 1

Sampling localities for juvenile Atlantic croaker. *n* is the number of individuals assayed from each locality.

Region and locality	Site	Collection date	*n*	Standard length (mm) mean (SD)	Standard length (mm) range
Atlantic					
Delaware Bay, Delaware (DE)	38°48'N 75°10'W	Oct 94	23	17.1 (1.8)	13–20
Cape Fear River, North Carolina (NC)	33°58'N 78°01'W	May 93	24	16.0 (1.9)	13–19
Indian River, Florida (FL)	28°03'N 80°35'W	Mar 94	22	19.4 (2.2)	16–23
Gulf of Mexico					
Terrebonne Bay, Louisiana (LA)	29°10'N 90°30'W	Jul 96	24	89.4 (4.5)	79–98

(RFLP) were used 1) to document the magnitude and spatial distribution of mtDNA variation in *M. undulatus* from U.S. Atlantic and Gulf of Mexico localities, 2) to evaluate the integrity of Cape Hatteras, North Carolina, as a genetic stock boundary, and 3) to estimate levels of gene flow among Atlantic localities to provide an improved basis for future decisions regarding coastwide management of this fishery resource.

Methods

Juvenile Atlantic croaker were collected from three U.S. Atlantic estuaries (Delaware Bay, Cape Fear River, and Indian River Lagoon) and one Gulf of Mexico estuary (Louisiana) (Table 1). Sampling localities were chosen to represent the northern, central, and southern portions of the species' U.S. Atlantic coast range and to include areas north and south of the hypothesized stock boundary at Cape Hatteras, North Carolina.

Genomic DNA extracts from individual croaker were obtained by using the Puregene DNA isolation kit (Gentra Systems, Inc., Minneapolis, MN) and were used in the polymerase chain reaction (Saiki et al., 1988) to amplify two mtDNA regions: the protein-coding ATP synthetase subunit 6 gene (ATPase 6) and the noncoding "D-loop" segment of the control region (Lankford, 1997). ATPase 6 was amplified by using the primers ATPase 6-L and ATPase 6-H (Quattro[2]), which yielded a 705-base-pair (bp) product. Primers L-Thr (5'-3': AGC TCA GCG CCA GAG CGC CGG TCT TGT AAA) and 12SAR-H (5'-3': ATA GTG GGG TAT CTA ATC CCA GTT) were used to amplify a 1540-bp product containing the entire D-loop region, tRNA-Pro and tRNA-Phe genes, and portions of the 12S rRNA and tRNA-Thr genes (Lee et al., 1995). Amplifications were performed in 50 μL reaction volumes according to Kocher et al. (1989). PCR products were digested with twelve restriction endonucleases: *Hinf*I, *Hae*III, *Msp*I, *Pvu*II, *Sau96*I, *Alu*I, *Mse*I, *Rsa*I, *Taq*I, *Dde*I, *Nla*III, and *Hha*I (obtained from New England BioLabs, Beverly, MA) (Lankford, 1997). Variant RFLP patterns were confirmed by means of repeat digestions and electrophoresis on 3% NuSieve agarose gels. Fragment sizes were estimated by using molecular weight markers: pUC18-*Hae*III digest from Sigma-Aldrich Corp., St. Louis, MO, pBR322-*Msp*I digest from New England BioLabs, Beverly, MA, and pBR322-*BstN*I digest from New England BioLabs; and the ANAGEL software program (Mrazek and Spanova, 1992).

Distinctive restriction-fragment patterns were identified by letter codes and subsequently combined to produce composite mtDNA haplotypes for individual fish. Nucleon diversity (h) was calculated for each locality (Nei and Tajima, 1981) with standard errors estimated according to Nei (1987). Nucleotide sequence diversity and nucleotide sequence divergence were calculated with the Restriction Enzyme Analysis Package (REAP, version 4.0) (McElroy et al., 1992). Frequency distributions of composite mtDNA haplotypes were tested for geographic homogeneity by using a Monte Carlo chi-square simulation approach (Roff and Bentzen, 1989) and a total of 10,000 random data resamplings. The integrity of Cape Hatteras as a genetic stock boundary was tested by comparing mtDNA haplotype frequencies north (Dela-

[2] Quattro, J. M. 1996. Department of Biological Sciences, Univ. South Carolina. Personal commun.

ware) and south (North Carolina and Florida) of this locality. Phylogenetic analysis was employed by using the character-state approach to construct a maximally parsimonious network relating individual haplotypes based on the number of restriction-site differences (Avise, 1994). The resulting network was examined for geographic structuring of haplotypes within and among sampling regions.

Population structure in *M. undulatus* was also evaluated by using nested analysis of molecular variance (AMOVA [Excoffier et al., 1992]). AMOVA input consisted of an Euclidean distance matrix containing genetic distance values for all possible pairs of the 15 observed mtDNA haplotypes. Samples were stratified by locality (DE, NC, FL, and LA) and nested within region (Atlantic or Gulf). Total genetic variation was partitioned into three components: within geographic localities, among geographic localities within the Atlantic region, and between regions. Significance of variance components was tested by using 10,000 random permutations to generate null distributions for each variance component. Gene flow among localities was estimated with Wright's (1943) island model, modified for mtDNA: $F_{ST} = 1/2N_e m_{\varphi} + 1$. Calculations employed Φ_{ST} as an approximation of F_{ST}.

Results

RFLP analysis of the ATPase 6 and D-loop regions revealed a total of 68 restriction sites. The average individual was scored for 62 sites and 264 nucleotide positions representing approximately 12% of the ATPase 6 and D-loop regions combined, or 1.6% of the entire mitochondrial genome. A total of 15 composite haplotypes was detected in *M. undulatus* (Table 2). Of the 93 individuals surveyed, 67 (72%) shared the same composite genotype (haplotype 1). Genetic distance among haplotypes averaged 0.17% for the pooled sample, with the most divergent haplotypes (10 and 12) differing from the common haplotype by only 0.75% and 1.0%, respectively.

Nucleon diversity (h) averaged 0.47 ±0.01 (mean ±SE) for the pooled sample, and ranged from $h = 0.25$ ±0.12 in DE to $h = 0.62$ ±0.12 in LA. Nucleotide sequence diversity also varied geographically, ranging from $\pi = 0.07\%$ in DE to $\pi = 0.32\%$ in LA. Net sequence divergence (p) among localities was low, indicating that most of the observed mtDNA variation occurred within localities. Average sequence divergence for the pooled sample was $p = 0.004\%$, with comparisons among Atlantic localities yielding slightly lower divergence values than comparisons involving Gulf and Atlantic samples. Croaker collected north versus south of Cape Hatteras were genetically indistinguishable (p=–0.002%) whereas nucleotide divergence between regions (pooled Atlantic vs. Gulf) was 0.005%.

Table 2

Geographic distribution (see Table 1 for specific locations) of composite mtDNA haplotypes among Atlantic croaker samples from Atlantic and Gulf of Mexico localities. Letters denote mtDNA fragment patterns (lowercase = ATPase 6; uppercase = D-loop) produced by digestion of PCR products with the following polymorphic restriction endonucleases: ATPase 6: *Pvu*II, *Alu*I, *Dde*I; D-loop: *Hinf*I, *Hae*III, *Msp*I, *Mse*I, *Taq*I, *Nla*III, *Hha*I.

Composite mtDNA haplotype	Haplotype frequency				
	DE	NC	FL	LA	Total
1. aaaAAAAAAA	20	16	16	15	67
2. bbaAAAAAAA	1	1	0	2	4
3. aaaAAAACAA	1	1	2	0	4
4. aaaAAAABAA	1	3	0	0	4
5. aaaAAAAAAB	0	1	0	0	1
6. aaaDAAAAAA	0	1	0	0	1
7. aaaABAAAAA	0	1	0	1	2
8. aaaBAAAAAA	0	0	3	0	3
9. aaaAAABAAA	0	0	1	0	1
10. aaaAAAABBC	0	0	0	1	1
11. aaaAAAAABA	0	0	0	1	1
12. aaaBBAAAAC	0	0	0	1	1
13. aaaAABAAAA	0	0	0	1	1
14. aabAAAAABA	0	0	0	1	1
15. aaaAAAAAAC	0	0	0	1	1
Totals	23	24	22	24	93

The common mtDNA genotype (haplotype 1) was numerically dominant at all localities (Table 2). The remaining 14 haplotypes occurred at low (<10%) frequencies. Monte Carlo tests for homogeneity revealed no significant heterogeneity in mtDNA haplotype frequency distributions within the SAB (NC vs. FL, χ^2=11.3, p=0.140) or among all Atlantic localities (p=0.148). When NC and FL samples were pooled and compared to the DE sample, there was no indication of heterogeneity among samples collected north and south of Cape Hatteras (χ^2=4.6, p=0.906). To further test for population structure within the Atlantic region, an additional 20 specimens from each Atlantic locality were screened for D-loop variation with the polymorphic enzymes *Taq*I and *Hha*I. Neither *Taq*I (χ^2=3.45, p=0.562) nor *Hha*I (χ^2=1.95, p=0.682) haplotype frequencies exhibited significant heterogeneity among Atlantic localities.

Given the lack of heterogeneity within the Atlantic region, composite haplotype frequencies were pooled across Atlantic localities and compared with the Gulf of Mexico sample. Monte Carlo simulations

Table 3

Hierarchical nested analysis of molecular variance on genetic distance between Atlantic croaker mtDNA haplotypes.

Variance component	df	Φ statistic	Variance	% total	P
Among regions (Atlantic vs. Gulf)	1	$\Phi_{CT} = 0.046$	0.021	4.6	<0.01
Among localities within Atlantic	2	$\Phi_{SC} < 0.001$	<0.001	<0.1	0.10
Within localities	89	$\Phi_{ST} = 0.046$	0.431	95.4	0.03

revealed significant heterogeneity between Atlantic and Gulf samples (χ^2=24.36, p=0.020) (Table 2). Parsimony analysis indicated that geographically segregated haplotypes were generally closely related (1–2 restriction site changes) to the common haplotype (Fig. 1). AMOVA revealed that the majority (95.4%) of mtDNA variation in Atlantic croaker occurred within samples (Table 3). A significant portion (4.6%) was attributable to regional differences (Atlantic versus Gulf, P<0.01) but variation within the Atlantic region was unstructured (p=0.10) and accounted for <0.1% of the total genetic variance. Φ_{ST} values indicated a lack of geographic structure and relatively high gene flow among Atlantic localities. Gene flow among Atlantic localities was estimated as 23.4 (DE and NC), 16.8 (NC and FL), and 12.0 (DE and FL) effective female migrants per generation.

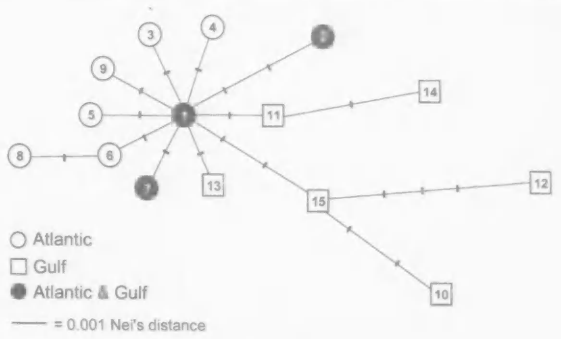

Figure 1

Parsimony network relating 15 mtDNA haplotypes observed in Atlantic croaker. Hatch marks drawn through each branch indicate the inferred number of restriction site differences among haplotypes. Branch lengths denote Nei's genetic distance between haplotypes (note scale).

Discussion

MtDNA analysis provided no evidence that *M. undulatus* is subdivided by Cape Hatteras into discrete genetic stocks. Frequency- and distance-based analyses both suggested a single, panmictic population of croaker on the U.S. Atlantic coast. Low levels of mtDNA divergence among Atlantic localities, although not statistically significant, were more consistent with a pattern of semi-isolation by distance rather than marked subdivision by Cape Hatteras. For example, AMOVA revealed that the two Atlantic localities exhibiting the least genetic divergence were DE and NC (Φ_{ST}=0.021; p=0.89). NC and FL samples were slightly more divergent but not significantly so (Φ_{ST}=0.029; p= 0.180). Lack of population structure was perhaps best indicated by the lack of differentiation between DE and FL samples (Φ_{ST}=0.040; p=0.084), two locations representing the distributional limits of this species' range on the U.S. Atlantic coast.

Kornfield and Bogdanowicz (1987) inferred patterns of gene flow from distributions of unique mtDNA haplotypes and their presumed precursors, predicting that under restricted gene flow, unique haplotypes should occur in the same population as their precursors. This was the case for *M. undulatus* at the regional (i.e. Atlantic versus Gulf) level, where unique Gulf haplotypes 10, 12, and 14 each had likely precursors that were confined to the Gulf region. Within the Atlantic region, however, unique haplotypes and their likely precursors occurred at disparate localities. The occurrence of rare haplotypes at more than one Atlantic locality also implies that genotypes arising at one locality spread rapidly to other localities within the Atlantic. Combined with low levels of nucleotide divergence, these observations support the hypothesis of contemporary gene flow among Atlantic localities. Gene flow estimates based upon Wright's island model are consistent with panmixia: values ranged from N_em =12.0–23.4, well above the theoretical lower limit of N_em = 1 sufficient to preclude genetic divergence of populations by random drift (Slatkin, 1985).

Previous studies have reported geographic variation in life history traits and population dynamics of Atlantic croaker found north and south of Cape Hatteras (White and Chittenden, 1977; Ross, 1988), suggesting that two groups of croaker with contrasting life histories overlap in the Cape Hatteras region, with a mainly offshore group north of Cape Hatteras which displays greater size-at-age, greater longevity, lower annual mortality, and delayed maturation in relation to croaker south of Cape Hatteras. A more recent study by Barbieri et al. (1994a) in the Chesapeake Bay concluded that life history variation in *M. undulatus* was ephemeral and that the two-stock hypothesis should be re-evaluated. The present mtDNA analysis supports previous suggestions by Ross (1988) and White and Chittenden (1977) that life history variation, when present, has an ecophenotypic basis.

A review of *M. undulatus* life history characteristics lends support to the panmixia hypothesis for the Atlantic region and provides several mechanisms by which trans-Hatteras gene flow may occur. Mark–recapture studies indicate extensive movement by *M. undulatus* along the U.S. Atlantic coast and thus potential for gene flow by means of adult migration (Pearson, 1932; Haven, 1959; Bearden, 1964; DeVries[3]). Larval dispersal could augment gene flow. Atlantic croaker larvae are abundant at outer-continental shelf locations (Govoni and Pietrafesa, 1994) and may spend more than 60 days in shelf waters before reaching estuaries (Warlen, 1980). Offshore spawning combined with an extended pelagic larval stage in shelf waters could provide ample opportunity for larval dispersal among Atlantic localities. Interestingly, spring recruits are occasionally reported in the mid-Atlantic Bight (MAB) estuaries as late as May and June (Haven, 1957; Chao and Musick, 1977) despite reports that spawning ceases in this area by late December (Morse, 1980; Barbieri et al., 1994b). Spring recruits to MAB estuaries may therefore be transported to mid-Atlantic estuaries from spawning sites south of Cape Hatteras. Thorrold et al. (1997) found no significant differences in otolith chemistry of juvenile croaker from the Neuse River, North Carolina, and the Elizabeth River, Virginia, suggesting that immigrants to estuaries north and south of Cape Hatteras may originate from the same spawning area. The reproductive strategy of *M. undulatus* may also facilitate gene flow. Atlantic croaker are multiple spawners with indeterminate fecundity (Barbieri et al., 1994b). Because spawning occurs during a southerly coastal migration during fall, females could commence spawning within the MAB and spawn multiple times during their southward migration, effectively distributing maternal half-siblings (mtDNA clones) over an extensive geographic range.

MtDNA heterogeneity between Atlantic and Gulf of Mexico localities suggests that these regions support separate populations of *M. undulatus*. The observed genetic break is consistent with a contemporary range discontinuity in southern Florida, where *M. undulatus* seldom occur south of Indian River on the Atlantic coast and are rarely encountered south of Tampa Bay on the Gulf coast (Nelson et al., 1991; Pattillo et al., 1997). Average sequence divergence between Atlantic and Gulf haplotypes (p=0.005%) was relatively low, however, suggesting that the phylogenetic break between Atlantic and Gulf stocks may be less pronounced in *M. undulatus* than in other marine fishes (Bowen and Avise, 1990).

This study represents the first attempt to identify population genetic structure in *M. undulatus* using DNA-level markers. The technique employed in our study proved sufficiently powerful to detect regional (Atlantic vs. Gulf of Mexico) population structure, but did not reveal structured genetic stocks of croaker within the Atlantic. The integrity of Cape Hatteras as a genetic stock boundary could be tested further by using fine-scale markers such as microsatellites, which have revealed genetic differentiation among fish populations that exhibit little mtDNA divergence. Alternatively, higher-resolution mutation-screening analysis or direct sequencing of the mitochondrial D-loop region might provide greater resolution of geographic structure than the RFLP technique employed here (Ong et al., 1996; Stabile et al., 1996).

Although mtDNA analysis did not indicate discrete genetic stocks of croaker within the Atlantic region, harvest stocks (see Gauldie, 1988) worthy of management consideration may exist. Because low levels of gene flow may produce mtDNA homogeneity between otherwise self-recruiting stocks, mtDNA is incapable of distinguishing between low (1%) and moderate (50%) amounts of mixing (Carvalho and Hauser, 1995). Delineation of harvest stocks will thus require more precise estimates of mixing than those obtainable from mtDNA analysis. Mark–recapture studies designed to quantify the level of adult migration across Cape Hatteras, combined with otolith-based microchemical analyses to examine larval dispersal patterns, could provide valuable information on the level of mixing between the MAB and South

[3] DeVries, D.A. 1986. Inshore Atlantic croaker tagging study. *In* J. L. Ross, D. A. DeVries, J. H. Hawkins III, and J. B. Sullivan, Assessment of North Carolina commercial finfisheries, p. 331–394. Completion report for Project 2-386-R, North Carolina Department of Natural Resources and Community Development, Div. Marine Fisheries, Morehead City, NC.

Atlantic Bight (SAB) areas and clarify the extent to which *M. undulatus* in these regions constitute self-recruiting groups.

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Otolith microstructure, age, and growth patterns of dolphin, *Coryphaena hippurus*, in the western Mediterranean

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Abstract.—The age and growth of dolphin, *Coryphaena hippurus*, has been determined in wild specimens between 14.4 and 124 cm fork length (FL) caught off Majorca (Balearic Islands, western Mediterranean). Also, several methods have been applied to validate the results obtained and to assess the aging techniques presently used. In accordance with the sexual dimorphism of this species, the length–weight relationship showed negative allometry in females and isometry in males. The high correlation between increment counts and known age in 75 reared larvae from 0 to 38 days old (number of increments = 0.3894+0.9846·days of age; r=0.98) indicated that the daily deposition of growth increments in sagittal otoliths and regular incremental formation begins on day one. This correlation validated the use of otoliths in the aging of 176 juvenile specimens between 16.5 and 58.5 cm FL, in which the minimum and maximum ages observed were 47 and 176 days, respectively. Nevertheless, the progressive increase in complexity with the ontogenic development of these structures suggests that this method may underestimate age in adult fish, probably owing to the loss of marginal zones of the otolith during the polishing process. Thus, from 150 specimens between 65 and 124 cm FL, the interpretation of annuli from scales gave ages up to 3 years old, whereas readings of otoliths in 36 specimens of the same size interval gave ages between 0 and 1 year old. Growth parameters were calculated from the age–length relationships of otolith and scale readings in juvenile and adult fish, respectively, and from the analysis of monthly length-frequency distributions, obtained in 1990 and 1991 during the exploitation of juveniles from 18 to 70 cm FL (n=4084). The values obtained for L_∞ ranged from 72.4 cm FL in unsexed juveniles and 110.0 cm FL in females both juvenile and adult, whereas k ranged from 1.6/year in juvenile and adult females and 2.5/year in unsexed juveniles. Although the results obtained were quite different owing to the different length and age range considered, similar results were obtained by comparing the growth performance index (F), and showed the rapid growth of the species.

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Dolphin (*Coryphaena hippurus* Linnaeus, 1758) (Pisces: Coryphaenidae) is an epipelagic, top-level predator species widely distributed in the tropical regions of every ocean (Palko et al., 1982). It migrates widely, and in warmer months increases its range to subtropical areas. Thus, it occurs seasonally in the Mediterranean from spring to autumn, when surface waters reach temperatures above 16–18°C (Massutí and Morales-Nin, 1995); mature specimens are occasionally caught in the swordfish (*Xiphias gladius*) fishery with surface longlines at this time, and immature juvenile fish are exploited by small-scale fisheries that deploy surrounding purse nets around fish aggregation devices.

Dolphin age and growth have been determined by means of scale annuli (Beardsley, 1967; Rose and Hassler, 1968), daily growth increments in otoliths (Oxenford and Hunte, 1983; Uchiyama et al., 1986), and modal progression analysis (Wang, 1979; Murray, 1985). In addition, some growth studies have been made of fish of known age reared in captivity (e.g. Hassler and Hogarth, 1977; Ostrowski et al., 1989; Benetti et al., 1995b). In the Mediterranean, available growth data on this species are related to morphometric relationships (Lozano-Cabo, 1961; Bannister, 1976) and rearing experiments (Reñones et al., 1992; Ayari et al., 1995).

The objective of this paper was to determine, for the first time in the Mediterranean, the age and growth patterns (including juvenile and adult phases) of *C. hippurus*. To support age and growth parameters estimated from readings of scales and otoliths, direct validation by means of rearing experiments and indirect validation based on length-frequency analysis were also applied. Otolith microstructure was analyzed to determine increment patterns and morphological changes during growth and to obtain more precise increment counts.

Material and methods

From May to November 1990 and 1991, fork lengths (FL) of adult specimens (n=150) were measured from longline catches. Sex was determined on the basis of the sexual dimorphism of the species (Palko et

al., 1982). Scales were collected above the lateral line, at the level of the pectoral fin, cleaned with 5% KOH, and mounted on slides. Interpretation of scale rings was carried out with a projector at 10× magnification by using the method described by Beardsley (1967). The scarcity of adult fish prevented the use of age validation methods; therefore the annual nature of the rings was established from validated ages from other areas (Beardsley, 1967; Rose and Hassler, 1968). Juvenile fish (n=4084) were measured from 65 samplings made between August and December of the same years from small-scale fishery catches. Total weight and sex were recorded for subsamples (adults n=68, juveniles n=282) selected to cover the size distribution of both sexes. Sagittal otoliths were removed, cleaned, and stored in distilled water. Unbroken otoliths (n=212) were embedded in epoxy resin and polished with a graded series of sandpaper and, finally, with 0.3-µm alumina paste. To improve clarity, otoliths were moistened with immersion oil for several hours before reading.

Otoliths have a complex structure, with convex sides, pronounced rostrum and antirostrum, and a demarcated sulcus that terminates in a V-shaped excisural notch (Oxenford and Hunte, 1983). We selected the dorsal side of the otolith to obtain a section with a complete increment sequence. Otoliths were read under a light microscope coupled to a high-resolution video camera and monitor system. Growth increments were counted from the core to the edge of the pararostrum (Oxenford and Hunte, 1983). Incremental counts were made by beginning at the first clearly defined mark that encircled the primordium, which defines the outer edge of the nucleus. Growth increments in juvenile fish otoliths were enumerated along a single axis. In adult fish it was necessary, however, to follow a circuitous path to complete a set of counts, following prominent increments laterally until an area with clear increments was found. Each otolith was read independently by two of the authors; results were accepted only if the readings were coincident or their difference was less than 5%. Growth increments were counted at 500× and verified at 1000×. Microstructural growth increments were studied on fish of 22–43 cm FL (n=28) with a scanning electron microscope (SEM). To highlight increment zones, the polished sections were etched for 30 seconds with a 0.1 N HCl solution, or for 60–90 seconds with a 0.2 M EDTA solution.

Von Bertalanffy growth parameters were estimated from age–length relationships obtained from scale and otolith readings by using the FISHPARM program (Prager et al., 1987). These parameters were validated by an independent length-based method by using the ELEFAN I procedure included in the ELEFAN software package (Gayanillo et al.[1]). Because L_∞ and k are inversely correlated, the growth performance index ($\Phi = 2\log L_\infty \log k$) was employed to compare growth rates (Munro and Pauly, 1983).

The temporal relation between ring number and age was determined by using larvae of known age, obtained from eggs spawned in captivity. Larvae hatched on 25 July 1994 and were reared through the juvenile stage up to 38 days, according to the method described by Kraul (1989). Water temperatures during the experiment ranged from 26° to 27°C, within the range of water surface temperature found around the Balearic Islands from June to August, when the species spawns (at 24–27°C; Massutí and Morales-Nin, 1995). The presence of early larval stages has also been reported in the study area during this period (Alemany and Massutí, 1998).

To establish the timing of first ring deposition and early otolith growth, larvae were sampled daily during the first 15 days. Afterwards, three samples were taken at intervals of 7–8 days until the juveniles were 38 days old. Larvae were preserved in buffered alcohol. The standard length (SL) of each larva was measured, and sagittal otoliths (n=93) were removed, cleaned, and mounted on slides with epoxy resin. The otoliths were read with an image analysis system connected to a microscope. An iterative semiautomatic system was employed for detection of increments, measurement of otolith radius, and age attribution. Increment clarity was improved by using polarized light, and enhanced digitized images were used for interpretation. Each otolith was read at least twice at 1000× magnification with an oil lens.

Daily periodicity of increments in reared specimens was validated by linear regression analysis of the relation between counts of otolith increments and days. The intercept and the slope were examined with Student's t-test. This method was also used to test the isometry in the allometric indices obtained by applying exponential regression equations to the length–weight relationships.

Results

The parameters of the length–weight relationship for females, males, and the whole population, including unsexed specimens, are shown in Table 1. Isometric growth was found in males (t-test; P>0.05), but for females and the population as a whole, a negative allometry was found (t-test; P<0.01).

[1] Gayanillo, F. C., M. Soriano, and D. Pauly. 1988. A draft guide to the complete ELEFAN. ICLARM Software Project 2, 70 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

Table 1

Length–weight relationship parameters estimated by exponential regression equations ($y = ax^b$) between fork length (cm) and total weight (g) in *Coryphaena hippurus*. n = number of specimens; SE = standard error of slope; r = correlation coefficient.

Population	n	a	b	SE	r
Females	192	0.0139	2.8983	0.0011	0.997
Males	154	0.0092	3.0187	0.0018	0.996
Total	350	0.0113	2.9605	0.0007	0.996

The sagittae of *C. hippurus* are small in relation to fish size and generally butterfly-shaped, although they display different structural patterns with ontogenic development. The larval otoliths are round and the development of the rostrum starts at 8 days (Fig. 1, A and B). The sulcal structure is formed in 12-day-old larvae (Fig. 1C); the rostrum and antirostrum were, on average, separated in 17-day-old larvae (Fig. 1D).

Otoliths prepared for SEM observation showed differences depending on the etching agent. The otoliths etched with EDTA had less clear growth increments than did otoliths etched with HCl. These differences might be due to high protein content in the otoliths, which collapsed when the aragonite crystals were completely removed with EDTA. Whole otoliths showed the presence of concentric laminations or ridges (Fig. 2A) which revealed that the core region grew by the deposition of successive layers on the inner side. Sections of otoliths showed the typical pattern of incremental and discontinuous units, which formed growth increments with variable widths depending on the otolith area (Fig. 2, B and C). Some rhythmic patterns were also evident with 7–14 increment groupings (Fig. 2, B and D).

Under the light microscope, otoliths revealed a pattern of alternating light and dark concentric rings surrounding a core, which was deposited at the earliest stages of development (Fig. 3A). The width of the increments varied from the core to the edge, with narrow increments near the center of the otolith and at the edge, whereas wider ones were laid down from the first to the third month of life (Fig. 3, B and C). These differences in increment width may reflect periods of differential growth. Larger increment patterns, or bands composed of groups of 7–14–28 increments, were also observed (Fig. 3B), suggesting lunar growth rhythms.

From 93 reared larvae of known age, a total of 75 otoliths (81%) could be read under the light microscope. These larvae measured 3.8–65.0 mm SL, and their otolith radii ranged from 10.7 mm (at day 0,

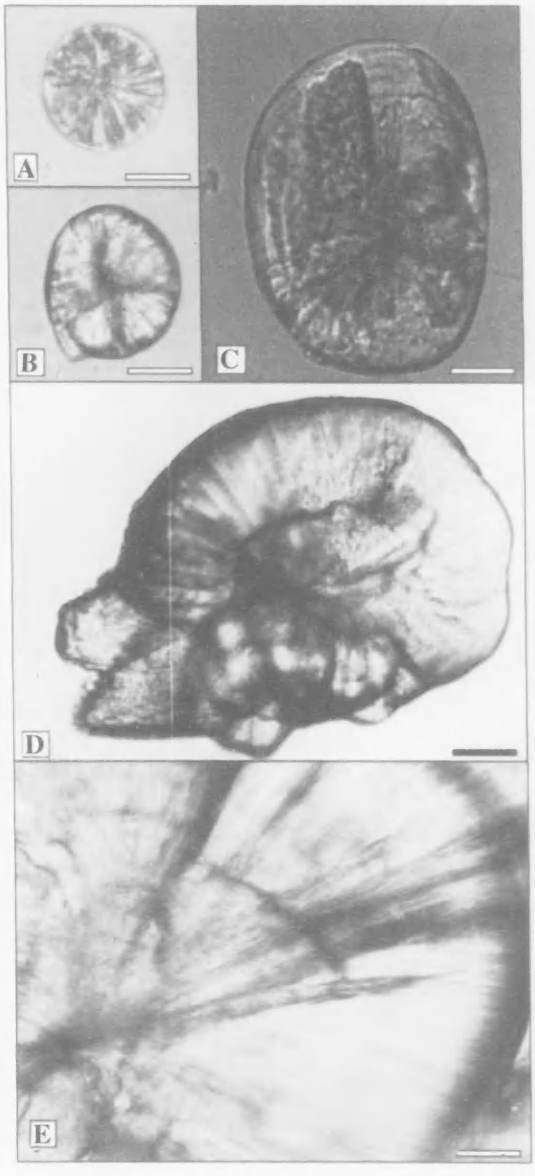

Figure 1

Photomicrographs of sagittal otoliths from *Coryphaena hippurus* larvae reared in captivity: (**A**) 6-day-old larvae of 6.1 mm SL (scale bar=25 μm); (**B**) 8-day-old larvae of 8.5 mm SL (scale bar=29 μm); (**C**) 12-day-old larvae of 8.8 mm SL (scale bar=34 μm); (**D**) 17-day-old larvae of 30 mm SL (scale bar=56 μm). (**E**) Poorly defined increments laid down around the core (scale bar=90 μm).

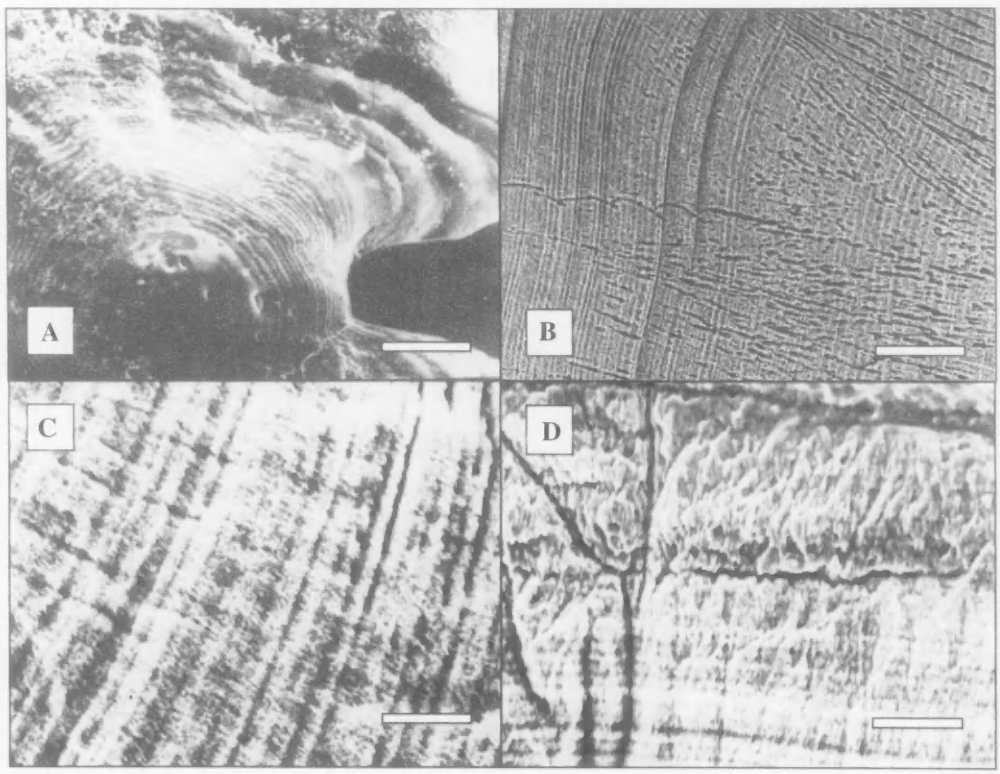

Figure 2

Scanning electron micrographs of *Coryphaena hippurus* sagittal otoliths. (**A**) Ridges on the surface of the central area of the otolith (scale bar=155 μm); (**B**) thin increments laid down in the central region of the otolith, showing rhythmic growth patterns of 7- and 14-increment groupings (scale bar=35 μm); (**C**) wider increments laid down in the outer region of the otolith (scale bar=10 μm); (**D**) rhythmic growth pattern of 14 daily growth increments (scale bar=15 μm).

n=1) to 20.6–23.9 mm (at day 36, n=3). In general, poorly defined concentric increments, consisting of an adjacent dark and a light zone, were laid down around the core (Fig. 1E). In relation between age in days and number of increments, neither the x-axis intercept nor the slope were significantly different from 0 and 1, respectively (t-test; $P>0.05$): $y = 0.3894 + 0.9846x$ (n=75, r=0.98).

From the juvenile fish, 125 otoliths were read (71%), 73 females between 19.5 and 58.5 cm FL and 52 males between 16.5 and 58 cm FL. Observed minimum and maximum ages were 47 and 176 daily growth increments. Of 36 adult fish otoliths studied with the light microscope, only 15 (42%) were able to be interpreted. A high percentage were rejected owing to error in reading precision greater than 5% or to erosion of the marginal zone during the polishing process. In specimens between 67 and 117 cm FL, the minimum and maximum ages read were 189 and 362 daily growth increments, respectively.

Scales from 139 adult specimens, measuring 65–124 cm FL, could be interpreted (93%). The results showed the presence of three age groups within the population: 67 1-yr-old specimens ranging from 65 to 110 cm FL ($\bar{x}$=87.95, SD=10.15), 61 2-yr-olds measuring 73–120 cm FL ($\bar{x}$=97.54, SD=10.95) and 11 3-yr-olds measuring 92–124 cm FL ($\bar{x}$=108.73, SD=10.17).

The von Bertalanffy growth function was calculated on the basis of the age–length relationships from daily growth rings in juvenile otoliths and annulae in adult scales (Fig. 4). Adult daily ages were not taken into account in these calculations because of observed underestimations in aging adults from

otoliths. Growth parameters for the whole population and by sex are shown in Table 2.

Length-frequency distributions for the 1990 and 1991 fishing seasons, based upon sampling of a fishery on juveniles, are given in Figure 5. Fish caught in this fishery from August to December measured 18–70 cm FL. The monthly length distribution indicated a rapid increase in the mode, mean, and minimum and maximum sizes for the catch. Von Bertalanffy growth parameters for this fraction of the population were estimated for the 1990 and 1991 fishing seasons (Table 2).

Discussion

The length–weight relationships obtained, showing negative allometric growth in females and isometry in males, are in accordance with the sexual dimorphism of *C. hippurus*. In this species there is a characteristic bullhead in males which, in the western Mediterranean, begins its development in individuals around 50 cm FL (Massutí and Morales-Nin, 1997). Similar results are obtained in other areas (Palko et al., 1982; Chatterji and Ansari, 1985), with a negative allometry that is stronger in females than in males.

Our study confirmed the daily nature of otolith growth increments in the first month of life for *C. hippurus* as reared fish. The strong correlation of mean sagittal counts to known fish age validated the use of otolith growth increments in the aging of juveniles up to 40 days old. Because regular incremental formation began on day one, no adjustment was required to estimate age from incremental counts of sagittae from wild fish.

Results suggest that the age of adult specimens is underestimated by the otolith method. This is clear when age–length relationships from daily growth rings in otoliths and from annuli in scales are plotted. For the same size interval, the otolith reading gave ages between 0 and 1 year, whereas interpretation of annuli in scales of adult fish gave ages to 3 years. This might be due to methodological problems in otolith preparation and interpretation. Consequently, the use of scales seems to be the best aging method for adult fish from the Mediterranean, from the point of view both of preparation and of results obtained.

The interpretation of juvenile fish age from daily growth increments seemed accurate, with a low percentage of disagreement between readers. To test the precision of this method, juvenile birthdate distribution was calculated by subtracting age in days from the date of capture. This showed a long period with peaks in the second fortnight of June 1990 and the first fortnight of July 1991 (Fig. 6). This small variation between years might be due to changes in the spawning peak or to differential mortality (Campana

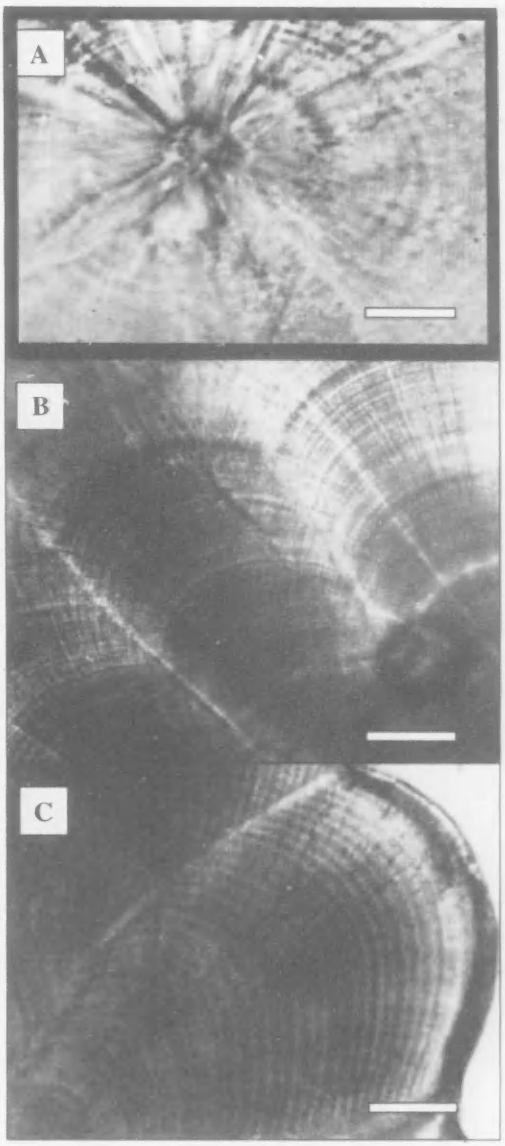

Figure 3

Light micrographs of *Coryphaena hippurus* sagittal otoliths. (**A**) Daily growth increments in the core region of the otolith (scale bar=15 μm); (**B**) narrow increments in the central region of the otolith, showing rhythmic growth patterns of 7-, 14-, and 28- increment groupings (scale bar=25 μm); (**C**) wider increments in the area of the otolith edge (scale bar=30 μm).

Table 2

Von Bertalanffy growth parameters for *Coryphaena hippurus* calculated by different methods. The standard errors of each parameter are in parentheses. n = number of specimens; L_∞ = asymptotic length (cm FL); k = growth coefficient in 1/yr; Rn = goodness-of-fit index; r = correlation coefficient; Φ = growth performance index. LFA is length-frequency analysis; S and O are scale and otolith readings.

Population	Sample	Method	n	L_∞	k	t_0	Rn	r	Φ
Juveniles	1990	LFA	2635	72.4	2.5	—	0.447	—	4.118
Juveniles	1991	LFA	1449	74.8	2.5	—	0.304	—	4.146
Females	1990–91	S and O	132	110 (2.62)	1.56 (0.14)	0.008 (0.02)	—	0.92	4.277
Males	1990–91	S and O	132	98.7 (1.59)	2.06 (0.19)	0.024 (0.02)	—	0.91	4.302
Whole	1990–91	S and O	264	102.4 (1.56)	1.90 (0.15)	0.023 (0.02)	—	0.87	4.300

and Jones, 1992). According to our results and those of Uchiyama et al. (1986), the deposition of increments in otoliths begins on the first day of life. In addition, ripe eggs hatch within 50–60 hours after fertilization, depending on temperature (Palko et al., 1982). Thus, hatching distribution can be compared with the spawning period of the species in the area, which is known from adult fish maturity data (Massutí and Morales-Nin, 1995, 1997). The agreement between these hatching dates and the above-mentioned data supports the daily ages determined from otoliths of wild juvenile fish.

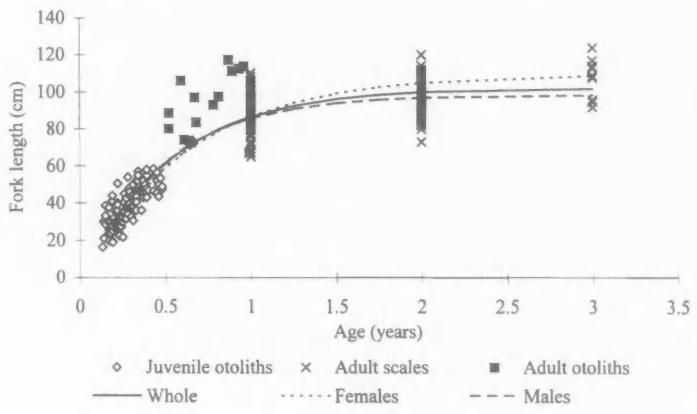

Figure 4

Age–length relationships and von Bertalanffy growth curves obtained from scale and otolith interpretation in *Coryphaena hippurus* adults and juveniles.

Another independent verification method uses link frequency analysis. The modal progression in juvenile catches showed a rapid growth rate, which is reflected by the almost double increase in monthly mean length during the fishing season from late August to early December. This rapid growth is in accordance with results obtained in the Mediterranean and other areas with reared specimens (e.g. Hassler and Hogarth, 1977; Reñones et al., 1992; Ayari et al., 1995; Benetti et al., 1995b), and with the estimates of growth rates between 3 and 10 cm per month, obtained from modal progression analysis on wild specimens in different areas (Wang, 1979; Oxenford and Hunte, 1983; Murray, 1985).

Growth parameters obtained by the two different methods used for the two population groups were quite different owing to the different length ranges considered. Nevertheless, similar results are obtained with the growth performance index. These values are similar to those calculated from growth parameters reported from scales of annuli by Beardsley (1967) and Rose and Hassler (1968), which were 4.27 and 4.19, respectively. Those calculated from growth parameters obtained by daily growth increments (Uchiyama et al., 1986) were slightly higher (4.52 for females and 4.63 for males), probably owing to the above-mentioned underestimation of age in adult fish with this method, the few adult specimens studied, and the effect of temperature on growth and metabolism. Temperatures can also explain the slower growth rate of *C. hippurus* in the western

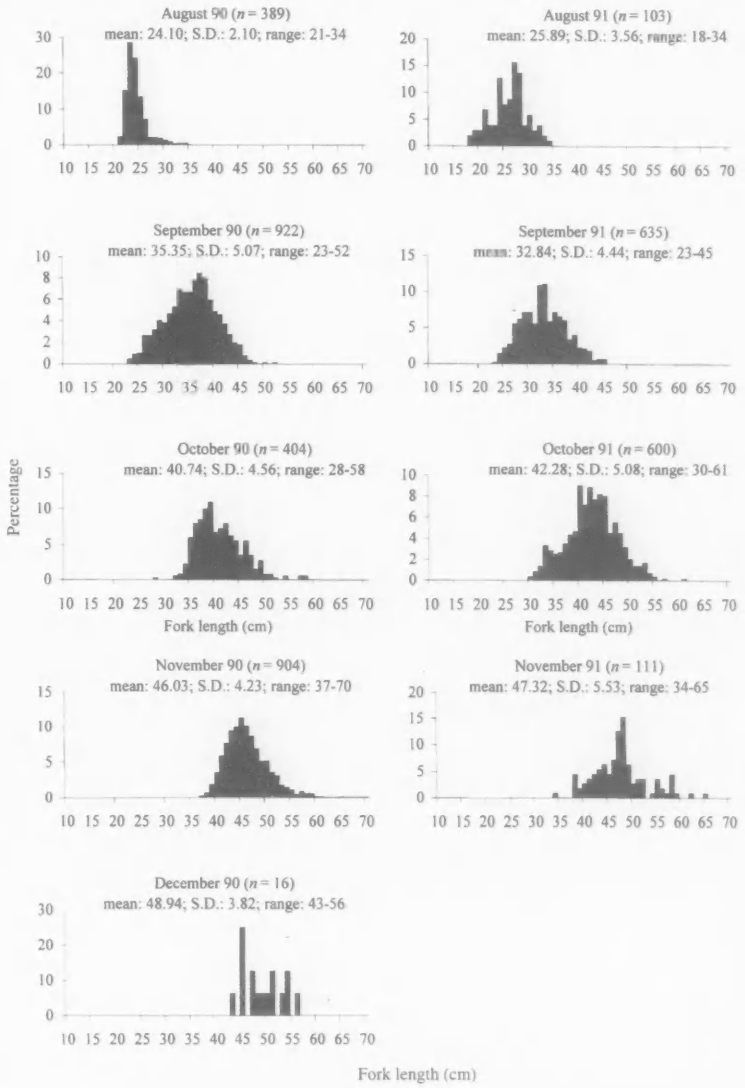

Figure 5

Monthly length–frequency distributions of juvenile *Coryphaena hippurus* caught off Majorca with the surrounding net during the 1990 and 1991 fishing seasons. Fork length in cm (*n*=number of specimens; SD=standard deviation).

North Atlantic Ocean (Beardsley, 1967; Rose and Hassler, 1968), where a decreased feeding rate when water temperature falls below 23°C and a cessation of feeding at 18°C have been reported (Hassler and Hogarth, 1977). By contrast, in Hawaiian waters, where faster growth rates have been reported, this species feeds throughout the year and can be expected to grow continuously (Uchiyama et al., 1986).

The growth-rate values obtained for *C. hippurus* are within the range reported from otolith microstructures by Brothers et al. (1983) for Atlantic bluefin tuna (*Thunnus thynnus*), another top-level predator characteristic of the western Mediterranean epipelagic ecosystem. According to Benetti et al. (1995a), *C. hippurus*, Scombridae species, and *Isurus oxyrhinchus*, another Mediterranean pelagic predator, have common factors

in environment and lifestyle which must strongly select for anatomical, biochemical, and physiological adaptations necessary to achieve exceptionally high metabolic rates. Such selection leads to high somatic and gonadal growth rates, rapid digestion, and quick repayment of oxygen debts, all important functions in these active pelagic predators.

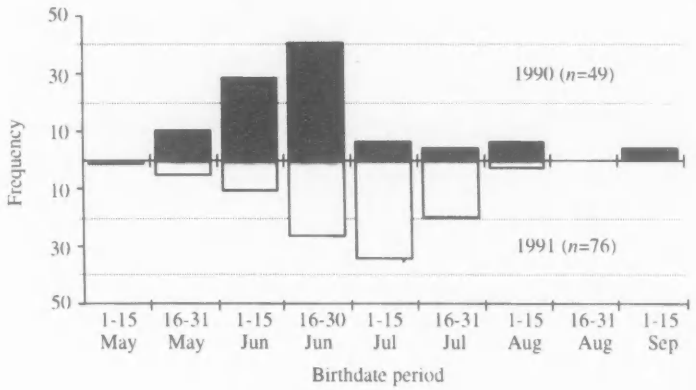

Figure 6

Frequency distribution of back-calculated birthdates for *Coryphaena hippurus* juvenile specimens in 1990 and 1991.

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Association patterns and inferred genealogies of resident killer whales, *Orcinus orca*, in Prince William Sound, Alaska

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Abstract.—The social structure and genealogical relationships of resident killer whale pods in Prince William Sound, Alaska, are inferred from association analysis and direct observation. During 1984–95 a total of 2444 hours of observation were made and 36,009 photographs were taken of identifiable killer whales. Cole's association index and a point correlation coefficient index were used to test the statistical significance and strength of associations between individuals, and a clustering procedure was used to delineate group structure. A total of 202 whales were grouped into 9 pods. Genealogical relationships were inferred from the strength of bonds among pod members. Genealogical trees suggested that intrapod groups were matrilineal in structure. Splitting of one pod (AN pod) was observed during the study; however, there was no splitting of matrilineal groups.

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It is well established that individual killer whales can be recognized by unique marks, scars, and pigmentation patterns (Bigg et al., 1987; Heise et al., 1992). During the past 25 years a number of studies have used this fact to investigate the life history, behavior, population dynamics, vocalizations, abundance, and movements of killer whales in coastal waters of the eastern North Pacific including Prince William Sound, Alaska (Balcomb et al., 1982; Bigg et al., 1990; Olesiuk et al., 1990; Ford, 1991; Matkin et al., 1994). As a result of these studies, at least two forms of killer whale, termed "resident" (fish-eating) and "transient" (mammal-eating), have been described in the nearshore waters of Puget Sound, British Columbia, and southern Alaska (Bigg, 1982; Leatherwood et al., 1990; Morton, 1990; Ford et al., 1998; Saulitis et al., in press). Although resident and transient killer whales occur sympatrically, they are considered separate populations owing to genetic variation in mtDNA haplotypes (Stevens et al., 1989; Hoezel and Dover, 1991) and microsatellite variation in nuclear DNA (Hoezel et al., 1998). Mating between the two forms has not been observed and resident and transient killer whales have not been seen traveling together (Morton, 1990; Saulitis, 1993; Matkin et al., 1994). Studies in British Columbia and Washington indicate that resident whales of both sexes remain in their natal pods for life, whereas transients appear to have a more fluid social structure (Bigg et al., 1990).

The social organization of resident killer whales in Prince William Sound has been previously described from direct observation of associations among individuals (Leatherwood et al., 1984; Heise et al., 1992). These studies name pods on the basis of observation of groups of individuals that repeatedly traveled together. Each identifiable whale is assigned an alphanumeric code (Leatherwood et al., 1984;

Ellis, 1987; Heise et al., 1992). The first letter in the code (A) designates Alaska, followed by a letter (A–Z) indicating the animal's pod as determined by observational data. Individuals within a pod are assigned sequential two-digit numbers. Pods that result from an observed splitting of a pod share letter designations, i.e. AN10 and AN20 pod.

In this study, we tested the hypothesis that Prince William Sound resident killer whales form nonrandom associations by examining the structure of some of the extensively studied pods in greater detail. Bond strength was established by direct observation of the proximity of whales to one another and by statistical analysis of the association of individuals in photographic sequences. We used statistical analyses to evaluate whether association patterns were random and used clustering techniques to describe underlying association patterns. Subsequently, we inferred genealogical relationships as an explanation for observed association patterns.

An understanding of social organization and genealogy is a prerequisite for studies of the sociology, life history, and population dynamics of Prince William Sound resident killer whales.

Materials and methods

Field methods

Field observations and photographs used in this analysis were collected from 1984 to 1995 in Prince William Sound, Alaska, and adjacent waters. Data were obtained throughout the Sound, although the study was centered in the southwestern portion. Field work occurred from April to October, but the greatest effort and the majority of encounters with resident pods occurred in July, August, and September. Vessels used to approach the whales to obtain photographs ranged in length from 4 to 9 m and in power from 50 hp outboard motors to 185 hp diesel inboard–outboard engines.

The techniques used to approach and photograph individuals were consistent over the duration of the study. During each encounter, individual whales were typically photographed several times from a distance of 15–30 m. Individual photographs were taken of the left side of each whale, showing details of the dorsal fin and gray saddle patch, with the technique developed by Bigg et al. (1986). An effort was made to move systematically through the pod and to obtain lateral-aspect photographs of individuals, such that each filled at least 50% of the frame. Photographs were taken during all behavioral modes and when whales were tightly grouped (i.e. resting) as well as when they were spread over a considerable distance (i.e. feeding). Encounters lasted until all whales were photographed or until weather or darkness (or both) made photography impracticable.

In the early years of the study we used a 35-mm SLR Nikon FM2 camera with an autowinder mounted on a shoulder brace. Later this setup was replaced by a 35-mm SLR Nikon 8008 autofocus camera with a shoulder brace. In all years a 300-mm lens was used and Ilford HP5 35-mm film was exposed and processed at ISO 1600.

Data recorded during each encounter with killer whales included date, time, duration, and location of the encounter. The total number of individuals present, the identity of individuals that could be immediately recognized, and the general behavior of the whales (i.e. feeding, resting, traveling, socializing, and milling) were also noted. Whales were considered associated on the basis of direct observation when they were seen traveling in the same direction and at the same speed for a period of greater than a few minutes and for a distance less than several body lengths.

Analysis of photographs

Throughout the study, each photographic frame was examined numerous times with a dissecting microscope to insure that all individuals were correctly identified (Bigg et al., 1987). Mothers of new calves were identified on the basis of consistent close association of calves with a specific female (Bigg et al., 1990). Identified individuals were recorded in a standard format to facilitate computer analyses, and uncertain identifications were excluded from the analysis.

Data analysis

In order to test the hypothesis that killer whales form nonrandom associations, associations between individuals were examined by using statistical analysis of photographic data. Photographs were placed in the order in which they were taken, and the identity of all individuals in each frame was tallied for each encounter. The analytical program examined associations between animals within photographic frames and in immediately adjacent frames. Photographic sequences that contained less than two individuals were deleted because they provided no information on association among individuals. Data from the remaining frames were accumulated in a 2×2 contingency table for each pair of whales for all years in which both individuals were photographed:

		First whale		
		Present	Absent	Total
Second whale	present	a	b	$a + b$
	absent	c	d	$c + d$
	total	$a + c$	$b + d$	n

where $(a + c)$ and $(a + b)$ denote the total number of occurrences of the first and second individuals respectively, a the number of joint occurrences, and d the total number of frames in which neither whale occurred in years in which both were photographed.

First, the degree of association between all individuals was measured by using Cole's (1949) association index (CAI):

$$CAI = \frac{ad - bc}{(a+b)(b+d)} \quad \text{for } ad > bc,$$

$$SE = \frac{(a+c)(c+d)}{n(a+b)(b+d)}$$

$$CAI = \frac{ad - bc}{(a+b)(a+c)} \quad \text{for } bc > ad \text{ and } d > a,$$

$$SE = \frac{(b+d)(c+d)}{n(a+b)(a+c)}$$

$$CAI = \frac{ad - bc}{(b+d)(c+d)} \quad \text{for } bc > ad \text{ and } a > d,$$

$$SE = \frac{(a+b)(a+c)}{n(b+d)(c+a)}.$$

The index was expressed as a percentage ranging from 100 to –100, with 100% indicating that the joint number of occurrences of each whale equaled the number of occurrences of the least-photographed individual. Zero percent indicated that the individuals were randomly distributed among photographs, and –100% indicated that the two individuals were never photographed together. The statistical significance of CAI values was evaluated according to their standard errors using Student's t test (Cole, 1949).

The CAI provides a measure of complete association (rather than absolute association) in that a value of 100% occurs only when the joint number of occurrences equals the number of occurrences of the less frequently photographed individual (see Cole, 1949, for details and a review of association indices). An index of complete association was deemed more appropriate for an analysis of patterns of association between individuals because not all individuals were equally identifiable (see Bigg et al., 1990) as was especially the case for cow–calf pairs, in which the often well-marked mother was generally identified in more photographs than her usually indistinct young calves even though they always traveled together.

Only CAI values for all years' combined were used to determine intrapod groups. CAI values were later calculated for the periods 1984–88 and 1989–95 and used to examine changes in bond strength between mothers and female offspring as the offspring matured and produced their own calves. The relationship between age of males and the bond strength with their mothers was also examined with these CAI values.

Groupings of individuals were identified from dendrograms constructed with an agglomerative average single-link algorithm (Johnson, 1967; see Fig. 1) In this procedure, CAI values for all possible pairs of individuals were compared and the pair with the highest CAI was linked. Then the pair of unlinked individuals with the highest CAI was linked, or an unlinked individual with a higher mean CAI value with previously linked individuals was linked to that pair, and so on until the mean CAI dropped to 20%. By this point, the vast majority of individuals had been linked into intrapod groups and we switched to an analysis with the point correlation coefficient (PCC):

$$PCC = \frac{ad - bc}{\sqrt{[(a+b)(a+c)(b+d)(c+d)]}},$$

where a represents the number of photographs containing one or more members of both groups, b and c represent the numbers containing members of only one or the other of the groups, and d represents the number containing no members of either group.

The PCC index, a measure of absolute association, was used to examine associations among intrapod groups determined by CAI analysis because each group was considered equally identifiable. The PCC index varies from 100% to –100%, with 0 indicating a random distribution. An index of absolute association was deemed to be more appropriate for intrapod groups because all groups contained readily identifiable animals; therefore observation of one group in the absence of another group indicated that each group was traveling independently of one another. The relationships among intrapod groups were examined from dendrograms constructed from PCC values with an agglomerative average single-link algorithm (see Fig. 2). Linkages with a positive PCC

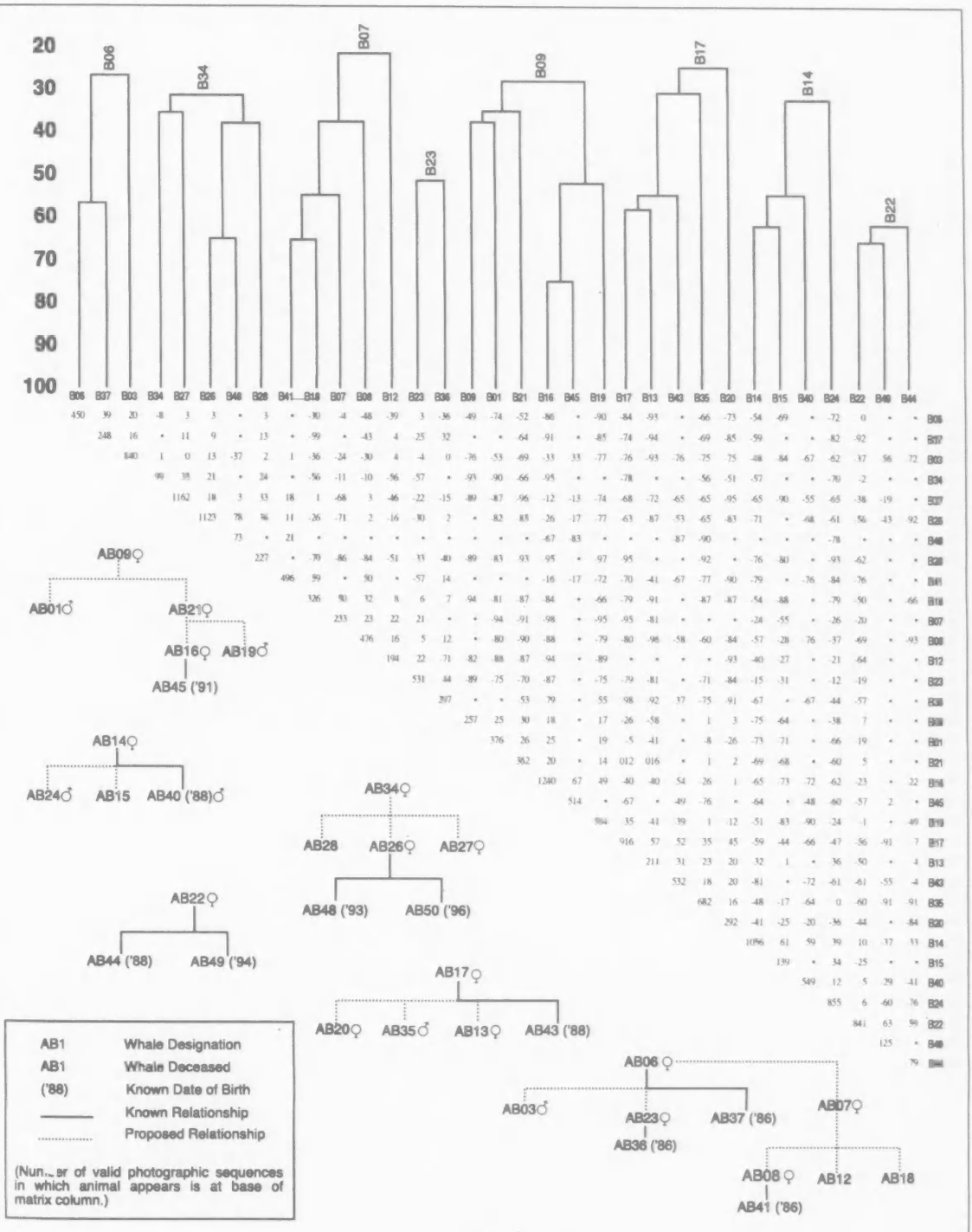

Figure 1

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups are shown in Fig. 2.) Middle: matrix of CAI values between pairs of individuals calculated at the pod level for AB pod, AB17 subpod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

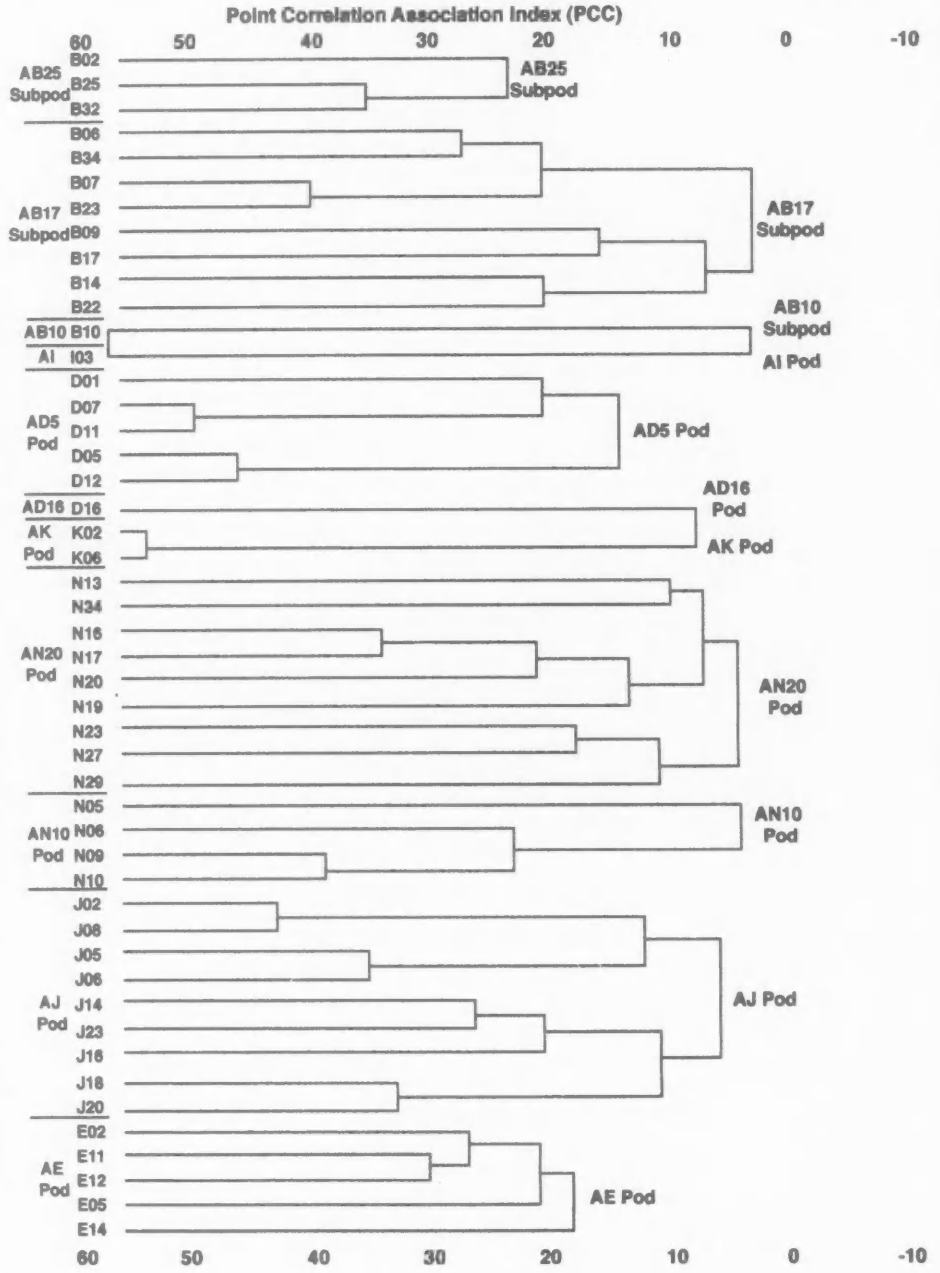

Figure 2

Dendrogram illustrating the relationships among intrapod groups (see top of Fig. 1 and Figs. 3–12) with values derived from PCC analysis.

association value (PCC>0) were designated as pods (Fig. 2). Groups were designated as subpods rather than pods when PCC values between them did not exceed zero but direct observation and photographic

summaries of encounters indicated that designated subpods traveled together as a single pod over 50% of the time.

Determination of sex and age

Sexually mature males were differentiated from females and immature males by their higher dorsal-fin height-to-width ratio (HWR), which typically exceeds 1.4 by 15 years of age (Olesiuk et al., 1990). Mature females were identified when they gave birth and were accompanied by a new calf. The sex of most juveniles could not be determined except in cases where the penis or the unique pigmentation pattern of the genital region was observed (Bigg et al., 1990; Olesiuk et al., 1990).

Actual ages could be determined for whales born during the study on the basis of their birth year. The ages of whales that were immature at the beginning of the study were estimated when they were first seen on the basis of relative size of the whale and size of the dorsal fin (Bigg et al., 1990). The approximate year of birth for whales that matured during the study was estimated by subtracting the mean age of maturity (15 years for both sexes) from the year they matured. Females were considered to have matured in the year they gave birth to their first viable calf, and males in the year in which their dorsal fin attained an HWR of 1.4 (Bigg et al., 1990; Olesiuk et al., 1990). The year of birth of males that were sexually but not physically mature at the start of the study was estimated by subtracting the mean age of physical maturity from the year their dorsal fin attained a HWR of 1.6–1.8, indicating physical maturity. Males that were physically mature and had a dorsal fin HWR of 1.6–1.8 at the beginning of the study were considered to be at least 21 years of age at that time. The minimum age of females that were mature at the beginning of the study was estimated by subtracting 15 years from the estimated birth year of their eldest offspring. This was a minimum estimate because a female's elder offspring may have died before the start of the study. Females that had not given birth for a decade or more were considered postreproductive (Olesiuk et al., 1990).

Construction of genealogical trees

Because statistical analysis indicated that whales associated in stable groups (or pods), CAI values were recalculated for all individuals within each pod and displayed in a matrix to show the relative strength of association among pod members (Fig. 1). We postulated that associations within pods reflected genealogical relationships and used them in conjunction with data on known relationships, sex and age data, and direct observations to infer genealogical relationships (Fig. 1).

Possible maternal genealogical trees were constructed in three steps (Bigg et al., 1990). Individuals to be incorporated into the tree as offspring were selected beginning with those born during the study, followed by those that were juvenile at the start of the study, and finally by those that were mature at the start of the study. Second, their potential mothers were identified. All mature females in the same pod were considered, providing that they could have been at least 12 years (minimum age of maturity) older. An individual's own mature daughters were excluded as potential mothers. Third, the relative strength of bonds as indicated by CAI values between the individual and all its potential mothers was examined. The potential mother with which the individual was most closely bonded was assumed to be its mother. An individual not strongly bonded to any potential mother was not assigned a mother. Matrices were cross-checked to insure that mother–offspring assignments created sibling groups that demonstrated reasonable linkage by CAI values. Direct observation was used to supplement statistical analysis to construct genealogies in instances where individuals and groups were less frequently photographed and where there was some ambiguity in the numerical analysis.

Results

A total of 2444 hours of direct observation of whales was logged from 1984 to 1995 (Table 1), during which 36,009 frames of film were exposed that were suitable for use in statistical analysis of association patterns (more than one individual appeared in the photographic sequence). A total of 202 whales photographed between 1984 and 1995 were included in the association analysis. According to direct field observations and inspection of photographs, these had previously been assigned to 9 pods (Table 2; Heise et al., 1992). Another 158 whales were tentatively grouped into 5 pods by field observation and visual inspection of photographs (pod AX, 54 whales; pod AY, 11 whales; pod AS, 17 whales; pod AF, 48 whales; pod AG, 28 whales). These pods were not included in the association analysis because there were insufficient photographs. The individuals listed in Table 2 represent the cumulative membership of pods over all years of the study. In all pods and most groups, the numbers of individuals varied over the course of the study as members died or were born during the study.

Table 1
Hours of direct observation and number of usable film frames by year.

Year	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	Total
Frames	6,076	1,284	2,967	1,326	1,400	3,549	5,940	3,701	3,641	2,333	1,662	2,130	36,009
Hours	307	154	127	91	92	268	423	246	255	127	120	234	2444

Statistical analysis indicated that individual whales did not associate randomly with one another. For individuals seen together at least once, 38.5% of all CAI values from the initial analysis of all individuals in all years were significantly less than 0 at a 5% confidence level (30.1% at a 1% level) and 27.5% were significantly greater than 0 at a 5% level (23.2% at a 1% level) (see Cole, 1949). Because these values are far greater than expected owing to chance, we rejected the null hypothesis that association patterns were random. The various animals positively associated with a particular individual tended to be positively associated themselves. These groups were also indicated by the agglomerative cluster analysis. A dendrogram showing associations among all 202 individuals included in the analyses was too large to exhibit here as a single figure; it appears split into pods along with matrices of CAI values and proposed genealogical trees for each pod (Figs. 1, and 3–12)

In nearly all cases, intrapod groups of individuals linked by association analysis at greater than 20% CAI reflected groupings established by direct observation. Direct observation also indicated that these intrapod groups virtually always traveled together. Most intrapod groups were centered around a reproductive or postreproductive female, which led us to suspect that these groups reflected matrilineal genealogies. However, in four cases single males (AE14, J02, N19, and D01) were not joined to other intrapod groups (CAI>20%) and in two cases pairs of males (AD02 and AD12, and AB02 and AB29) were linked to each other but not to other intrapod groups (CAI>20%). The nine pods examined contained 48 intrapod groups, including male singles and pairs (Figs. 1 and 3–12). With the exception of AB pod, pods comprised 1–9 intrapod groups. Two pods (AI and AD16) contained only one intrapod group. The three subpods of AB pod contained a total of 12 intrapod groups. Intrapod groups were composed of 1–9 individuals.

Patterns of association between intrapod groups, as indicated by statistical analysis, generally supported the pods constructed by direct observation. Forty-six of the 48 intrapod groups (190 of 202 individuals) were linked at the zero level of association into their respective pods (Fig. 2). There were two exceptions; repeated direct observations were used to clarify separations into intrapod groups. First, the AB10 subpod was linked in the dendrogram with AI pod (PCC=4) before it was linked with the other subpods of AB pod. Second, AK pod and AD16 pod formed distinct clusters as expected but were joined at the PCC = 8 level, which was greater than the zero level adopted to define the other pods.

Table 2
Pods and individual whales used in this analysis.

Pod	Cumulative membership
AB	AB01-AB51
AI	AI01-AI07
AJ	AJ01-AJ38
AE	AE01-AE20
AK	AK01-AK14
AN10	AN01-AN03, AN05-AN12, AN35,AN38, AN40-AN41, AN45-AN51
AN20	AN04, AN13-AN34, AN36-AN37, AN39, AN42-AN44
AD05	AD01-AD12, AD19,AD21-AD27
AD16	AD13-18, AD20

On the basis of direct observation, AN10 pod and AN20 pod were considered a single pod (AN pod) until 1989, when they began traveling separately a majority of the time. AN whales were encountered on 46 occasions during 1984–88; the AN10 and AN20 groups were observed together in 35 (76%) of these encounters. In contrast, during 1989–95 they were observed together in only 3 of 65 (5%) encounters where AN whales were present. After 1992 they were not seen traveling together and were thus designated as separate pods. The association analysis supported their designation as separate pods (Fig. 1). AD pod was also considered a single pod early in the study on the basis of direct observation during a few encounters. From more recent direct observation and the results of the association analysis, it is now designated as two pods (AD5 and AD16 pods).

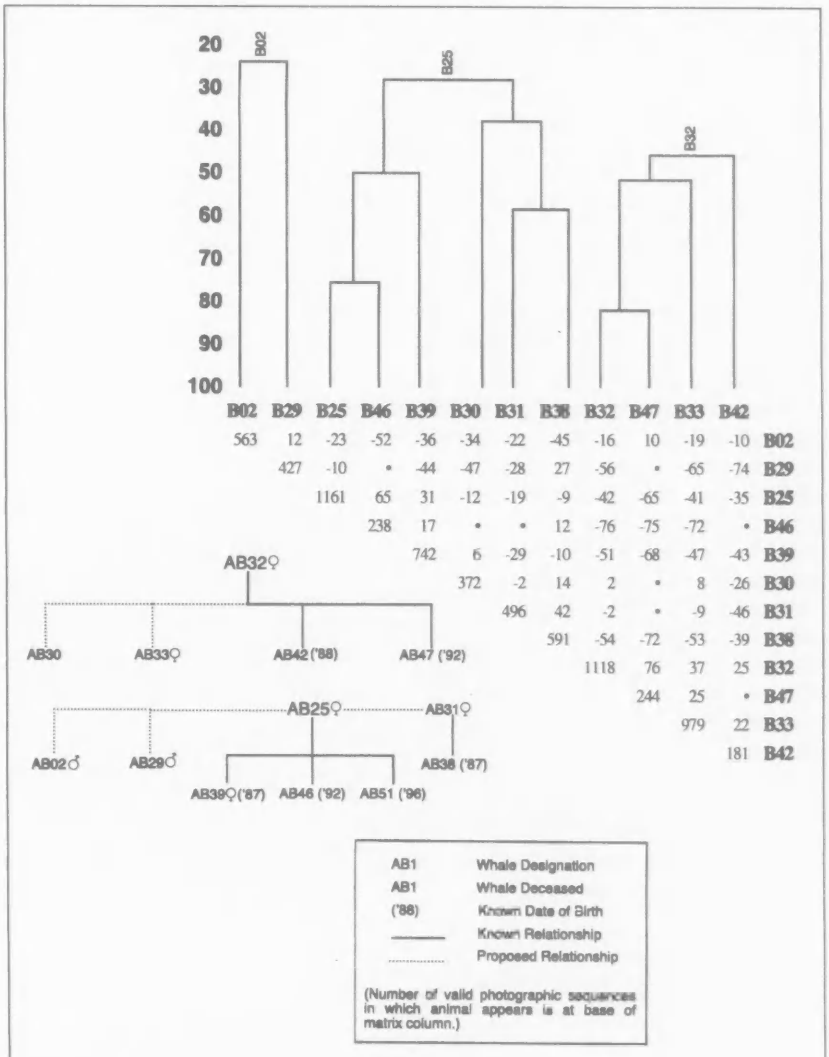

Figure 3

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AB pod, AB25 subpod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

On the basis of lack of linkage in the PCC dendrograms above the zero level, AB pod was divided into three subpods (AB10, AB17, AB25), although prior to 1994, direct field observations indicated that these subpods very rarely traveled separately. However, even when traveling together, the subpods typically traveled as cohesive units within the pod. Since 1994, direct observation has indicated that the AB25 subpod has split off and travels mainly with AJ pod. Other than those established for AB pod, no other subpods were identified in the study.

To explain association patterns within intrapod groups, we postulated that these represented matrilineal groups and that genealogical relationships

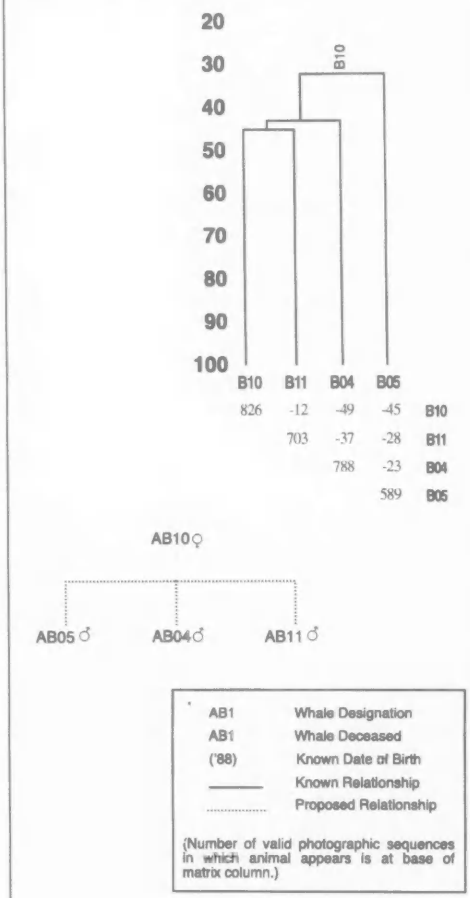

Figure 4

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 12.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AB pod, AB10 subpod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

could be deduced by examination of bond strengths within these groups. CAI values were calculated between all individuals of each pod and dendrograms of the CAI values were constructed to reveal the structure of associations between the members of each pod (Figs. 1, and 3–12).

The individuals in the nine pods examined in the second CAI analysis were placed in 39 postulated maternal genealogical trees on the basis of linkages established in association analysis. An additional four newborn calves were observed in 1996 and placed in the genealogical trees on the basis of field observations only. Genealogical trees were constructed by first establishing all known mother–offspring relationships from field observations. There were 58 offspring born during the study that appeared in the photographs used for association analysis. In all but one case (AB41 and mother AB8), the CAI values between offspring and their known mothers was higher than for any other pairings of individuals. Direct observation also indicated that offspring maintained their strongest bonds with their known mothers throughout the study period. The three offspring born at the beginning of the study were still most strongly bonded to their mothers after 12 years. These were mother–offspring pairs AI3 and AI4 (CAI=27); AK6 and AK8 (CAI=34); and AE11 and AE13 (CAI=46).

Table 3

Cole's association index (CAI) values for mothers and female offspring that produced their first calf in 1987 or later.

Reproductive offspring	Year of first calf	Mother	CAI 1984–1988	CAI 1989–1995
AJ3	1990	AJ8	28	13
AJ4	1994	AJ8	57	20
AJ13	1992	AJ14	40	33
AK7	1993	AK6	51	24
AN10	1987	AN9	22	-20
AN11	1992	AN9	30	23
AN26	1990	AN23	53	34
AN31	1990	AN20	28	19
AN35	1988	AN9	29	2

The strength of the bond between females and their mothers declined in the nine cases in which females became reproductive during the study and their mothers remained alive throughout the study (Table 3). A paired t test of CAI values for 1984–88 and CAI values for 1989–95 showed that the tendency for associations to decline after female offspring become reproductive was statistically significant (t=4.88, P=0.0012).

There were 31 juveniles (estimated age 10 years or less in 1984) at the beginning of the study. Association analysis indicated that all but five of these whales remained most closely bonded to the whales judged by direct observation to be their mothers. Three of these exceptions were females that produced calves (AK7 and calf AK12; AN8 and calves AN41

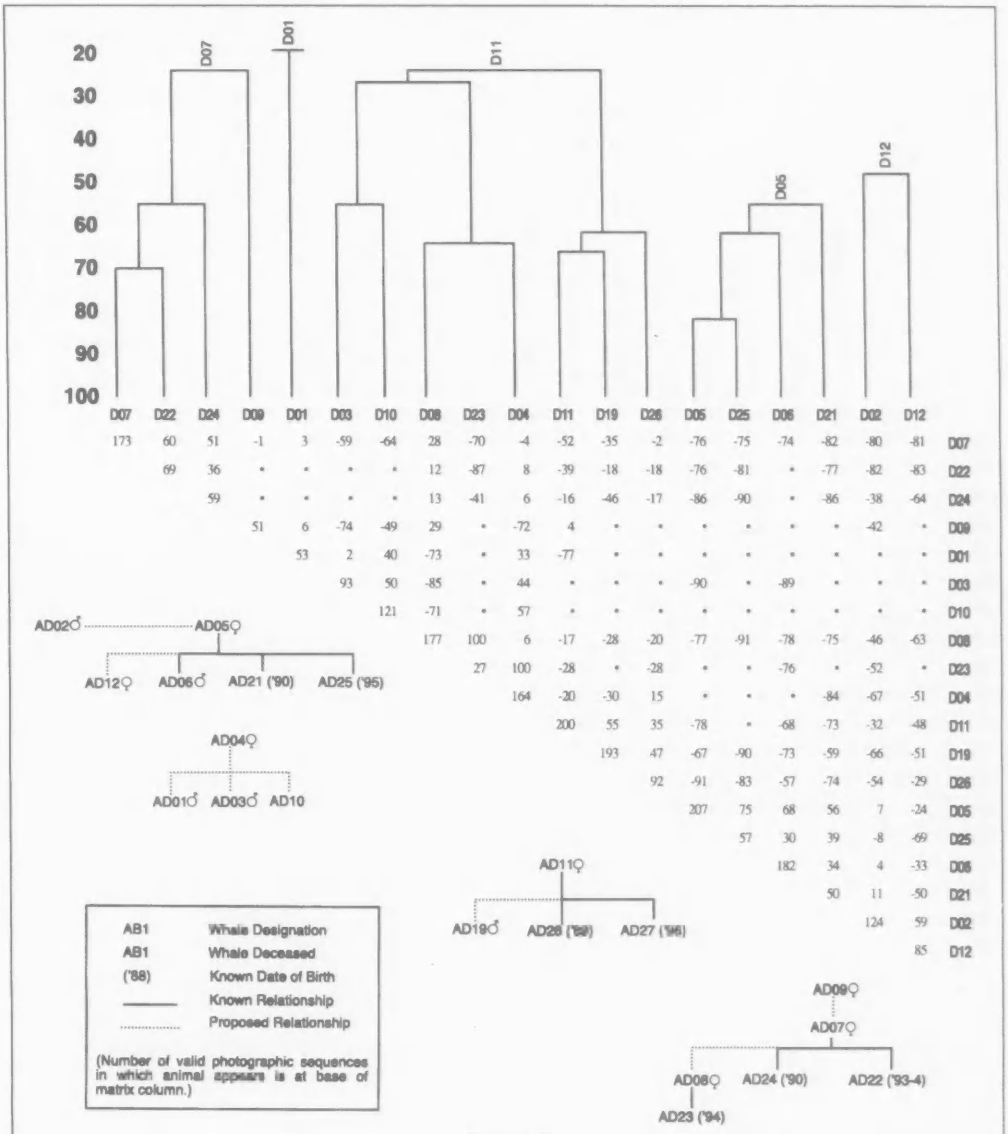

Figure 5

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AD5 pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

and AN48; AN11 and calves AN47 and AN49). These females became most closely bonded to their own calves rather than to their mothers. One juvenile male, AN19, had a stronger bond with apparent juvenile sibling AN18 (CAI=16) than with his apparent mother, reproductive female AN17 (CAI=4). The juvenile AB18 had a stronger bond (CAI=58) with a young calf, AB41, in his intrapod group than with his apparent mother, reproductive female AB7 (CAI=22). However, in the cases of all five of these whales, the strongest bond with an adult female remained with their apparent mothers.

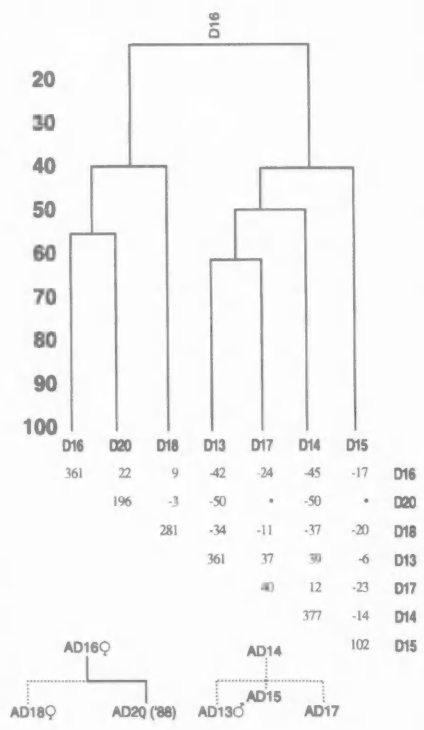

Figure 6

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AD16 pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

The strength of bonds between male offspring and their mothers was highly variable (Table 4). Simple regression analysis indicated that the strength of bonds tended to diminish with age, but not significantly ($F_{1,27}$=1.62; P=0.215).

Table 4

Cole's Association Index (CAI) values for male killer whales and their mothers. Ages estimated as described in methods; ages over 20 years are mimimum ages.

Whale	Estimated approx. age (yr)	CAI Value	Whale	Estimated approx. age (yr)	CAI Value
AB1	33	25	AJ9	18	32
AB3	30	20	AJ16	27	48
AB24	25	39	AJ17	29	18
AB35	19	35	AJ21	19	31
AJ25	22	48	AK4	27	29
AD3	27	50	AK1	27	20
AE1	32	25	AN3	32	31
AE3	18	21	AN7	24	17
AE6	16	38	AN14	19	47
AE14	19	24	AN21	25	54
AE9	32	31	AN24	15	55
AJ1	31	39	AN25	24	28
AJ2	27	21	AN30	16	54
AJ7	19	55	AN33	23	41
AN1	32	66			

Of the 45 proposed maternal lineages (Figs. 3–12), 25 included two generations, 16 included three generations, and four had four generations. In all but one of the four-generational trees, the oldest matriarch died during the study. We identified four matrilineal intrapod groups that appeared destined to die out. These were the single adult male, AB3 (Fig. 4); the AB10 subpod which consisted of the apparently postreproductive female AB10 and 3 adult male sons, AB4, AB5, and AB11 (Fig. 6); the apparently postreproductive AJ12 and her adult male son, AJ16 (Fig. 9); and the apparently postreproductive AN 34 and her adult male son, AN21 (Fig. 10). Three of the remaining matrilineal groups had produced two reproductive females in one generation and were growing, and eight had produced one reproductive female and were relatively stable. The fate of the other matrilineal groups will be determined later as offspring born during the study mature and their reproductive potential is realized.

Discussion

Direct observations indicated that resident killer whales in Prince William Sound do not associate randomly with one another, but rather tend to associate with specific individuals. Statistical analysis of associations in photographic sequences supports this

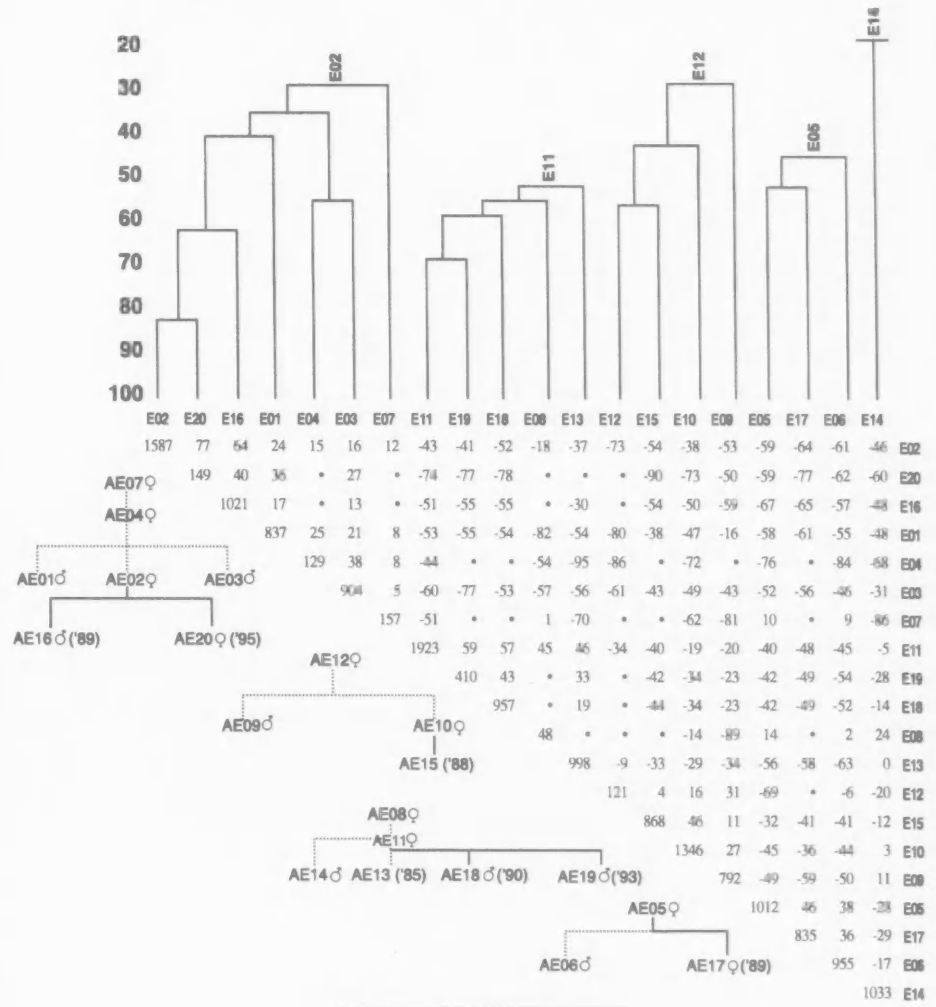

Figure 7

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AE pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

observation. It is important to appreciate that in this analysis (Fig. 1 and subsequently Figs. 3–12), results were obtained by using a continuous clustering process in which all whales were treated as individuals

and were linked into progressively larger groups until they formed a single large group. This analysis examines the relationships between individuals in the entire population.

We postulate that the significant long-term associations observed were based on genealogical relationships. Judged from known relationships (mothers and offspring born during the study), the strength of bonds among individuals within pods appeared directly correlated with their degree of relatedness.

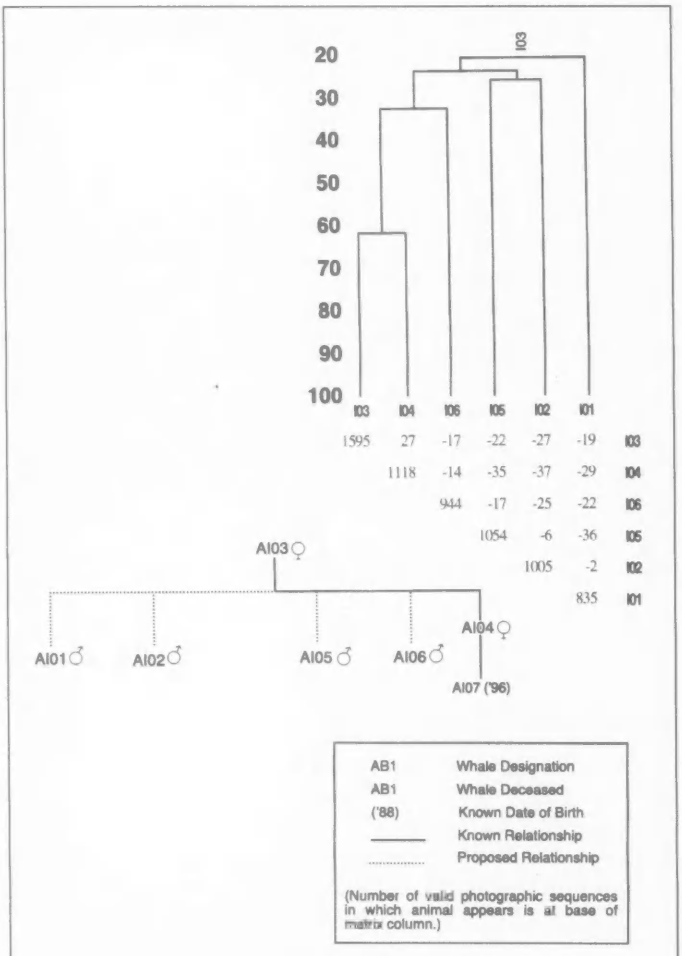

Figure 8

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Figure 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AI pod. Numbers at the base of each column in the matrix are the numbers of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

Our findings that resident killer whales in Prince William Sound are organized in statistically identifiable pods and intrapod groups are similar to results from studies of resident killer whales in British Columbia and Washington State (Heimlich-Boran, 1986; Bigg et al., 1990). Bigg et al. (1990) defined a pod as a group of individuals that traveled together at least 50% of the time. All the resident pods described in Prince William Sound fit that definition. Pod membership is also supported by pod-specific vocal dialects in both areas (Bigg et al., 1990; Ford, 1991; Ford[1]).

Pod delineations based on direct observation were supported by association analysis in all but two cases. Both discrepancies appeared in the final stages of the agglomerative linking procedure. Although each pod was a distinct cluster, AD16 pod was found to be linked to AK pod with a PCC value of eight, at somewhat higher than the level of linkage between other pods. This was not supported by direct observation and was apparently an artifact of small sample size. AD16 pod was infrequently photographed and was often part of multipod groups that included AK pod.

The AB10 subpod was linked with AI pod (PCC=4) before being linked with other members of AB pod. AI pod frequently traveled with AB pod early in the study, and we suspect that AI pod (7 whales in 1996) was in the final stages of a gradual split from the then 35-member AB pod when the study began in 1984. AI pod traveled more independently of AB pod in later years. The pod-specific dialects for AI and AB pods are very similar (Ford[1]), supporting this hypothesis. The preponderance of adult males in AI pod (4 out of 7 whales in 1996) may have contributed to the independence of this matrilineal group. Bigg et al. (1990) found that matrilineal groups with a high percentage of males tend to travel more independently. This was also evident for the AB10 subpod, in which 3 out of 4 members were adult males. AB10 subpod often traveled a distance away from the remainder of AB pod.

Direct observation and photographic analysis also indicated that some males

[1] Ford, J. K. B. 1997. Vancouver Public Aquarium, P.O. Box 3232, Vancouver, B.B., Canada. Personal commun.

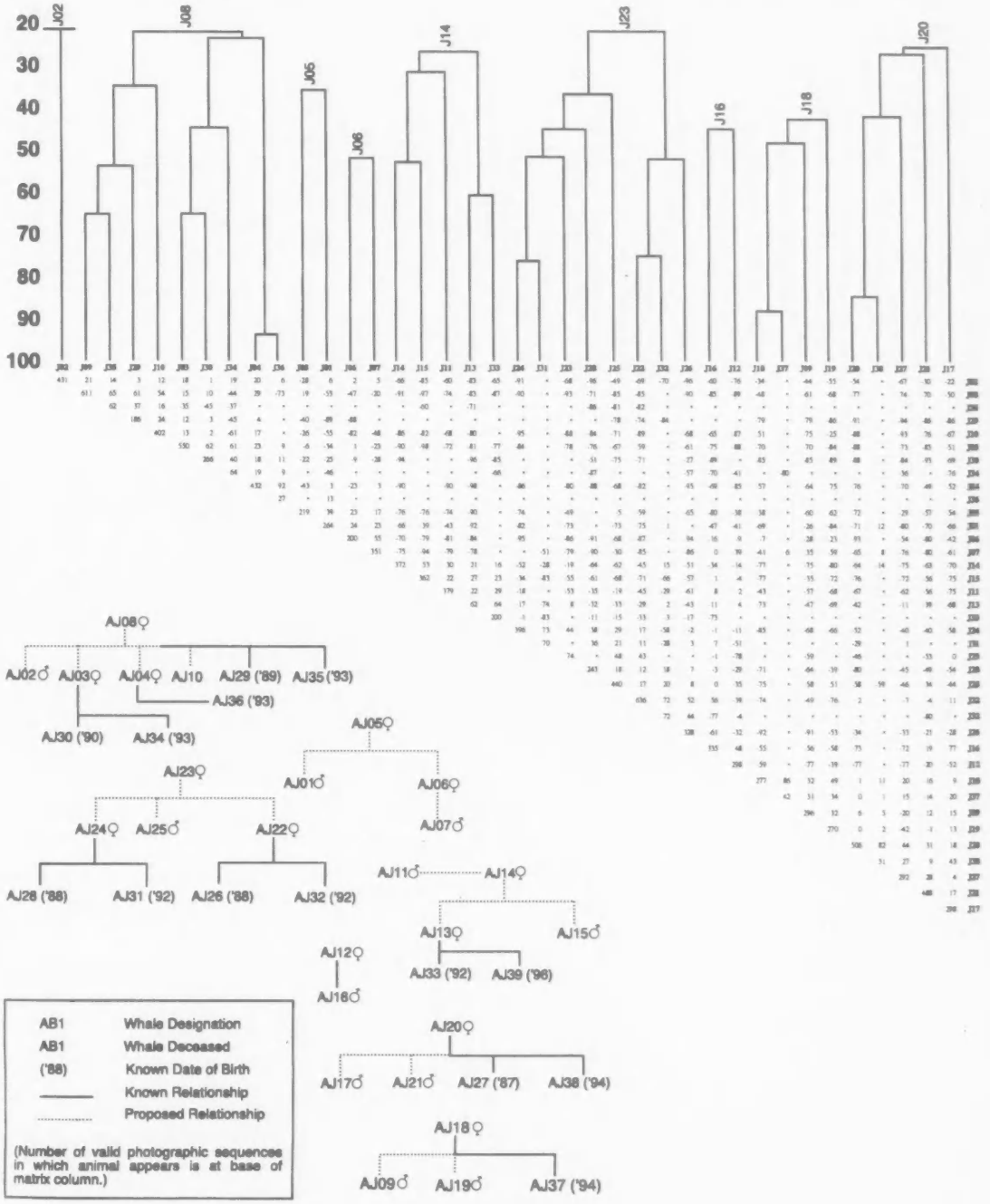

Figure 9

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AJ pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

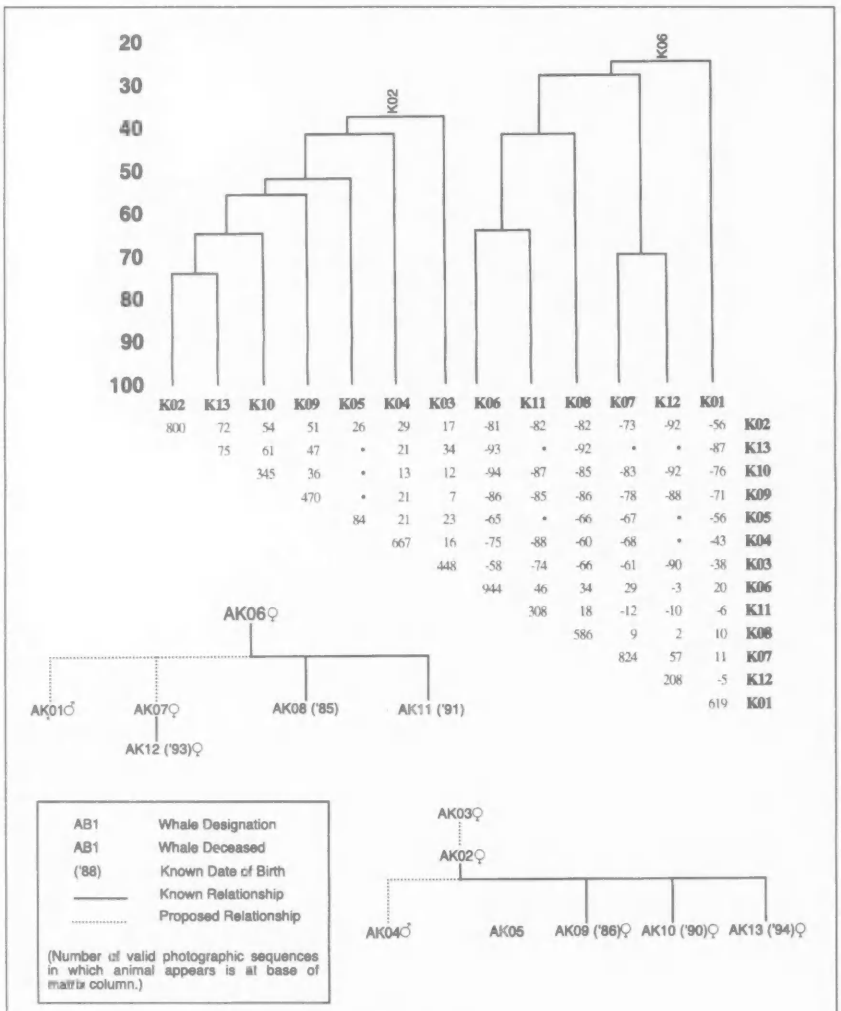

Figure 10

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AK pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

occasionally traveled with other adult or juvenile males or traveled independently, particularly during the multipod encounters observed in July and August (Matkin et al., 1997). In two cases, pairs of males were more highly associated with each other than with any other intrapod groups.

We witnessed the splitting of one pod (AN pod into AN10 and AN20 pods) during the course of the study. This was not a gradual occurrence, as suggested by Bigg et al. (1990) for A04, C01, and D01 pods in British Columbia but appeared to be a rather abrupt event around 1989. The pod split along intrapod (matrilineal) groups, while all 13 of the intrapod groups in the two pods remained intact. AN pod numbered 35 whales at the time it split and was the largest pod in the study at that time.

Bigg et al. (1990) defined subpods as fragments of pods that occasionally split and traveled separately

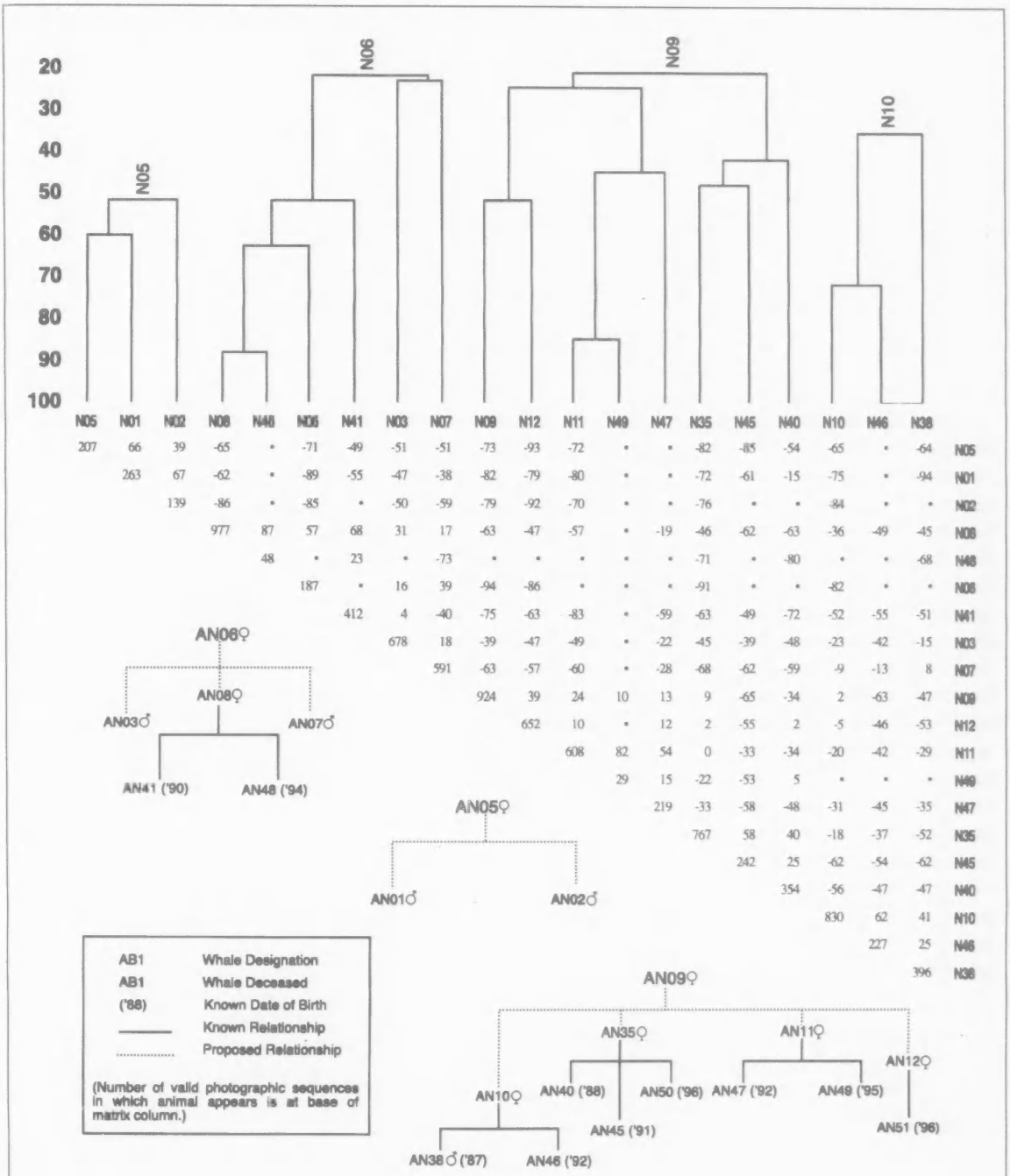

Figure 11

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AN10 pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

from their pods. Through association analysis, we expanded this definition to include groups that travel in unison with their pod but rarely mix with other groups within the pod. This latter situation occurred only for AB pod, which was divided into three subpods. By direct observation and examination of

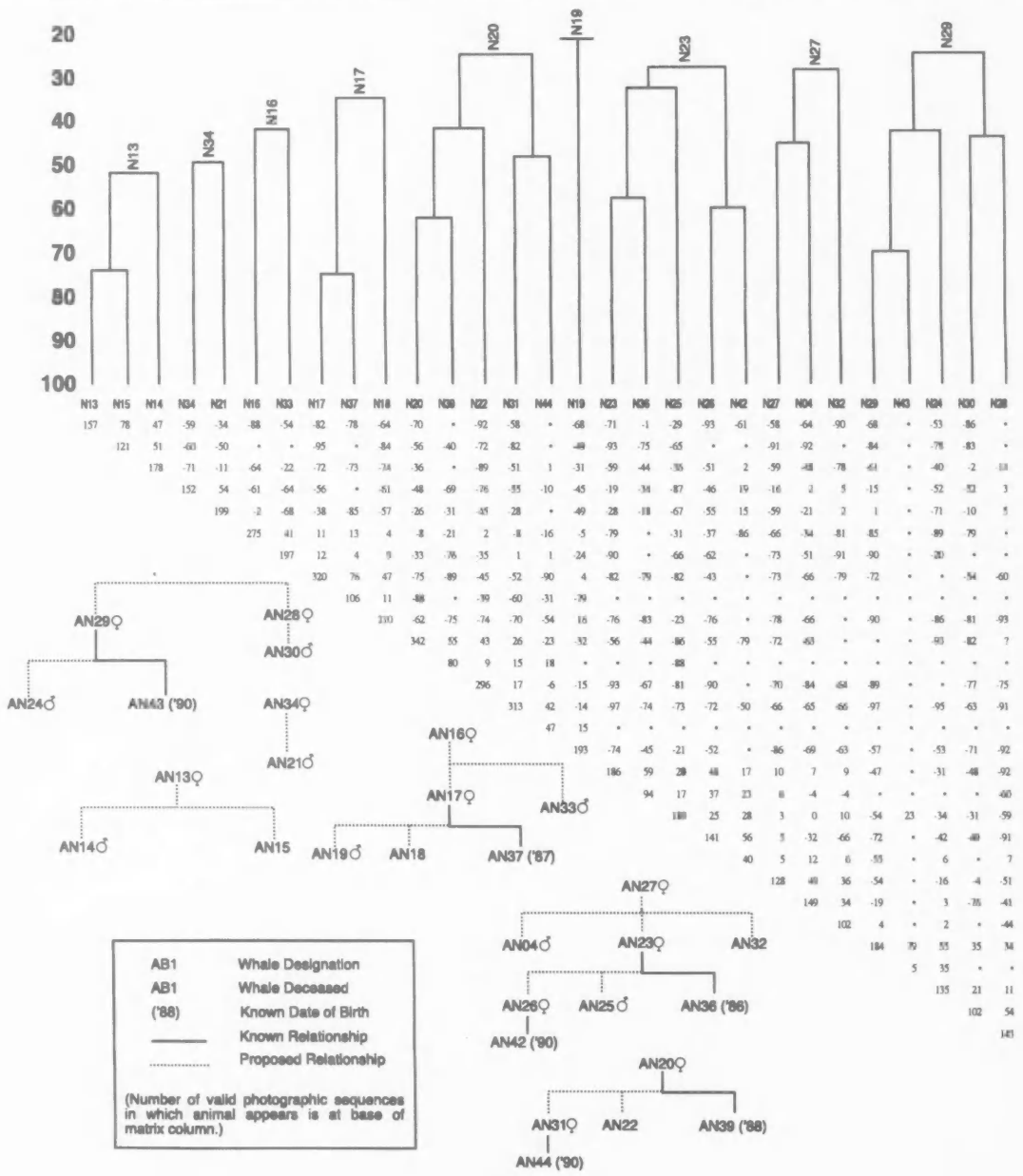

Figure 12

Top: dendrogram illustrating intrapod groups and relationships among individuals with CAI values calculated at the population level. (Relationships among intrapod groups shown in Fig. 2.) Middle: matrix showing CAI values between pairs of individuals calculated at the pod level for AN20 pod. Numbers at the base of each column in the matrix are the number of valid photo sequences in which that individual appears. Bottom: inferred genealogical trees.

photographs of this pod, it was determined that AB pod nearly always traveled as a unit; however, in the dendrogram linking intrapod groups (Fig. 2) it appeared as three separate groups (PCC>0). This finding indicated that although they were traveling together, the subpods tended not to mix with the rest of the pod.

Communities were described by Bigg et al. (1990) as closed populations of pods that associated with one another. They described two geographically distinct communities of resident killer whales (northern and southern residents) that had separation in range near the middle of Vancouver Island, British Columbia. We found no separation of pods into communities by this definition in our area, although our study discerned matrilineal (intrapod) groups, subpods, and pods. Resident whales from AF and AG pods photographed regularly in southeastern Alaska were observed swimming with the pods described in this study (Matkin et al., 1997). One of the pods described in this paper, AD5 pod, was photographed off Kodiak Island. It thus appears that geographic boundaries do not delineate communities for resident killer whales from southeastern Alaska to Kodiak Island.

The association analysis for individuals within pods strongly suggested that strength of bond was directly correlated to degree of relatedness. There was only one case in which statistical analysis indicated that offspring born during the study did not maintain the strongest bond with its mother. The mother AB8 and her sibling AB18 both died at the time of the Exxon Valdez oil spill. AB8 left her year-old offspring, AB41 (born 1988). Association analysis indicated that AB41 was more closely linked (CAI=58) to its mother's apparent sibling, AB18, than to its mother, AB8 (CAI=50); the young whale AB41 died several years later (1993–4).

Five whales that were juveniles at the beginning of the study were most closely associated with whales other than their mothers. Three were females, AK07, AN08, and AN11, each of which produced offspring during the study. Following these births, they were more closely bonded to their offspring rather than to their own mothers. This finding demonstrates that new mothers, when they produce calves, develop distance from their own mothers (Table 4). The tendency of females with offspring to travel farther from their mothers than the distance prior to first reproduction suggests a process of separation that may also be basic to new pod formation.

Our proposed genealogical trees suggest that intrapod groups are matrilineal groupings of mothers and their descendants (Figs. 1 and 3–12). There was no immigration or emigration of male or female offspring from these natal groups over the course of our study. These extremely stable matrilineal groups appear to be the foundation of resident pod social structure in Prince William Sound. This is similar to results from studies in British Columbia and Washington State (Bigg et al., 1990).

We were most confident in genealogical trees for pods that were most frequently photographed, such as AE and AK pods, and less confident in trees for the much less frequently observed AD5 and AD16 pods. The large number of mortalities in AB pod also made construction of genealogical trees more difficult. The greatest potential source of error in genealogical assignment was the death of the mother of a young whale prior to the study, in which case the young whale would likely travel with its closest female relative. However, since the annual natural mortality rate for reproductive females is extremely low (0.0048 according to Olesiuk et al., 1990), this source of error was probably insignificant except following disasters such as the high loss of reproductive females after the Exxon Valdez Oil Spill (Matkin et al., 1994).

In all but one of the resident pods we examined, the total number of whales increased over the period of the study, indicating that a majority of matrilineal groups have been growing or dividing (or doing both) over the past decades. The exception was AB pod, which declined during this period from 35 to 23 whales (28 deaths; 16 births). Six of the mortalities occurred during 1985 and 1986 when there was a conflict with the sablefish (*Anaplopoma fimbria*) fishery (Matkin et al., 1994). During this period apparent bullet wounds were observed in 16 whales.

Fourteen of the mortalities in AB pod occurred in the year and a half following the 1989 Exxon Valdez oil spill (Matkin et al., 1994). Some of the matrilineal groups in the pod are nearly extinct as a result of these deaths. An adult male, AB03, appears to be the last member of a once-large matrilineal group linked by the apparent sisters AB06 and AB07 (Fig. 1; AB03 has since died). Another large matrilineal group (matriarch AB09) has been reduced to a single orphaned 5-year-old, AB45. Many of the mortalities have been those of juveniles (13) or reproductive females (4) and have severely reduced the reproductive potential of the pod.

The statistical support for the existence of intrapod groups and the apparent lack of emigration or immigration into these groups allows for determination of demographic changes, both natural and induced, within resident killer whale populations. The detailed delineation of social structure in resident killer whales provides a unique opportunity for monitor-

ing and modeling of these populations. This situation appears to be unique among social mammals (e.g. the lack of male dispersal), with the possible exception of the long-finned pilot whale. In that species, molecular typing revealed that pod members also form extended family groupings from which individuals do not disperse (Amos et al., 1993). Molecular typing of individual whales described in this study is currently in progress (Barrett-Lennard[2]).

Acknowledgments

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Vertical distribution of eggs and larvae of northern anchovy, *Engraulis mordax*, and of the larvae of associated fishes at two sites in the Southern California Bight

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Abstract.—We studied fine-scale vertical distribution of northern anchovy, *Engraulis mordax*, eggs and larvae and larvae of associated species at two stations off southern California in March–April 1980 using a Manta (neuston) net and a MESSHAI (multiple opening-closing net) sampler. A pump and fluorometry system was used to obtain chlorophyll profiles. A storm with associated heavy seas interrupted sampling for two days at the inshore station and provided an opportunity to compare pre- and poststorm egg and larval distribution and abundance. A total of 95,552 fish larvae were taken in the MESSHAI (63 tows) and Manta nets (41 tows), representing 49 taxa (genera or species) in 27 families. *Engraulis mordax* was the most abundant fish (95% of the total), followed by *Leuroglossus stilbius*, *Genyonemus lineatus*, *Stenobrachius leucopsarus*, *Sebastes* spp., *Seriphus politus*, *Peprilus simillimus*, *Paralichthys californicus*, *Citharichthys* spp., and *Merluccius productus*. Anchovy eggs and larvae had a shallow distribution: 90% of larvae and 95% of eggs were found in the upper 30 m. Peak egg density was found in the neuston; peak larval density, in the 10–20 m stratum. Larvae of shallow-living shelf species (*G. lineatus*, *P. simillimus*, *P. californicus*) typically occurred in the upper 20–30 m, whereas larvae of predominantly deeper-living demersal species (*Sebastes* spp., *M. productus*) were found in the upper 80 m. Midwater species (*L. stilbius*, *S. leucopsarus*) occurred at least to 200 m. Anchovy eggs decreased in number after the storm. Anchovy larvae declined even more sharply, despite an increase in zooplankton and potential larval fish prey, suggesting that starvation may have resulted from disturbance of microscale food patches. Alternatively, larvae may have been advected away from the site. Shallow-water shelf species were rare at the inshore station before the storm but appeared suddenly afterwards as a result of seaward advection of shelf water by Ekman transport.

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The use of ichthyoplankton techniques for estimating the biomass of fish stocks has increased markedly over the past two decades (Hunter and Lo, 1993). Information on the horizontal and vertical distribution of eggs or larvae of a target species is a requirement for quantitative sampling of these stages and for interpreting data from integrated net tows and from recently developed samplers such as the continuous underway egg pump (Checkley et al., 1997). The daily egg production method (DEPM) was developed at the Southwest Fisheries Science Center to provide annual biomass estimates needed to manage northern anchovy, *Engraulis mordax*, an important coastal pelagic species inhabiting the California Current region (Lasker, 1985). During the development of this method a cruise was conducted off southern California that employed a MESSHAI, a sampler with opening-closing nets and environmental sensors, to determine fine-scale vertical distribution of eggs and larvae of *E. mordax* (see preliminary data in Pommeranz and Moser, 1987). This information was needed to supplement Ahlstrom's (1959) vertical distribution study based on 22 Leavett net tows taken on 9 cruises over a 14-year period off southern California and Baja California. The MESSHAI study supplied information on depth, ambient temperature, and diurnal periodicity of *E. mordax* eggs needed to develop the DEPM (Lasker, 1985). To compare distributions at different bottom depths, sampling was conducted at two localities: an offshore site over the Santa Catalina Basin and an inshore site over the upper continental slope off Dana Point, California. Anchovy larvae, the dominant species in the MESSHAI samples, were counted and measured for subsequent growth and mortality studies. A storm interrupted sampling at the inshore station and provided an opportunity to study the influence of water column disturbance on the abundance and depth distribution of eggs and larvae of anchovy and associated species. Mullin et al. (1985) described the effects of this storm on the abundance and vertical structure of phytoplankton, zooplankton, and total fish larvae on the basis of pump samples taken at the same time as the MESSAI sampling at a locality

just shoreward of the inshore MESSHAI site.

This paper presents a preliminary analysis of the fine-scale vertical distribution of anchovy eggs and larvae and the larvae of other taxa, with comparisons of the offshore and inshore sites and of the prestorm and poststorm periods at the inshore site. A separate paper addressing age-specific vertical distribution and mortality of anchovy eggs and larvae is in preparation.

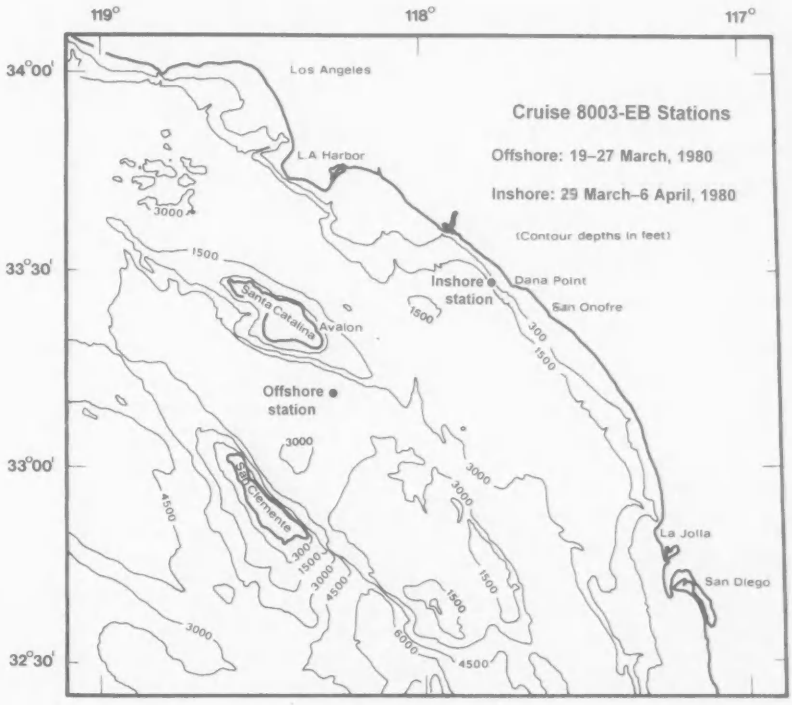

Figure 1

The Southern California Bight, showing stations occupied on Cruise 8003-EB (modified from Shepard and Emery, 1941).

Methods and materials

Cruise 8003-EB was conducted aboard RV *Ellen B. Scripps* at two sampling sites in the Southern California Bight (SCB; Fig. 1). The first site (33°11.1'N, 118°16.5'W), occupied 19–27 March 1980, was located 13 km south of the east end of Santa Catalina Island, over an ~1150 m bottom depth. This site lies over the Santa Catalina Basin, one of 13 deep basins that characterize the offshore region of southern California (Ebeling et al., 1970; Eppley, 1986). The midwater fish fauna of these basins is a mix of subarctic, transitional species of the California Current and species from the eastern tropical Pacific and central water masses whose distributions extend into the region. The site is close enough to Santa Catalina Island to have larvae of shelf species (Hobson and Chess, 1976) in addition to larvae of slope and basin floor species (Cross, 1987). The second site (33°28.5'N, 117°47.0'W), occupied 29 March–6 April 1980, was ~4.5 km off Dana Point, over the upper continental slope at approximately 430 m bottom depth. Here the adjacent shelf narrows to a minimum of about 3 km but supports rich fish communities associated with rocky reefs and kelp forests (Feder et al., 1974; Cross and Allen, 1993) and soft-bottom habitats (Mearns, 1979; Love et al., 1986; Allen and Herbinson, 1991; Cross and Allen, 1993). The continental slope, also relatively narrow here, supports a fish assemblage typical of other southern California slope regions (Cross, 1987). The first site corresponds to California Cooperative Oceanic Fisheries Investigations (CalCOFI) station 90.2, 35.8 and the second to station 90.0, 28.2. Sampling at the offshore station was interrupted twice by heavy seas (0055, 21 March to 0908, 23 March; and 1730, 26 March to 0836, 27 March). A storm with associated heavy seas curtailed sampling at the inshore site at 0315, 1 April; the station was reoccupied at 0655, 3 April.

The principal samplers used were the Manta net (Brown and Cheng, 1981) for sampling the surface layer (0–15.5 cm) and the MESSHAI for sampling discrete depth strata in the upper 200 m. The MESSHAI sampler was a modified Gulf-V sampler (Arnold, 1959; Nellen and Hempel, 1969) with a 25×25 cm mouth opening, six opening and closing nets operated from a computer deck unit, and an environmental sensing package (Pommeranz and Moser, 1987). All nets were fitted with 300-μm mesh. A sampling sequence for a day or night station consisted of a five-minute Manta tow, followed by an oblique MESSHAI tow that sampled 10-m strata from 50 m to the surface, an oblique MESSHAI tow which sampled 40-m strata from 200 m to the surface, a second MESSHAI tow which sampled 10-m strata from 50 m to the surface, and a second Manta tow. A total of 17 Manta tows (10 day, 7 night) were taken at the offshore station, 24 (13 day, 11 night) at

the inshore station (Figs. 2 and 3). All MESSHAI tows were stepped oblique hauls. In the shallow tows the sampler was lowered to 50 m and retrieved through five 10-m strata, each in 2.5-m steps lasting two minutes, with a total of five horizontal phases per stratum. Depth, temperature, and flowmeter profiles were recorded by the deck unit throughout each tow. Bucket surface temperatures were taken periodically to calibrate the MESSHAI temperature sensor. In the deep tows the sampler was lowered to 200 m and retrieved through five 40-m strata, each in five steps lasting two minutes. The total number of successful MESSHAI tows was 24 (shallow: 9 day and 8 night; deep: 4 day and 3 night) at the offshore station and 36 (shallow: 12 day and 12 night; deep: 6 day and 6 night) at the inshore station. Improper preservation or breakage resulted in the loss of anchovy eggs in net 4 (20–30 m stratum) of tow 42 and the entire sample from net 3 (30–40 m stratum) of tow 61. Three MESSHAI tows were unsuccessful owing to technical difficulties, and the samples were subsequently discarded. All tows were made at a ship speed of ~1.5 knots. Before each net tow series at the inshore station, a pump and fluorometry system (Lasker, 1978) was used to obtain a chlorophyll profile down to 40 m depth. Water samples were taken at the surface and at the chlorophyll maximum for chlorophyll-*a* and phaeophytin extraction and fluorometry, and for identification and counts of major phytoplankton taxa (analyses not included in this paper). Oblique bongo net samples were taken at each station at a ship speed of about 1.5 knots; except for length-frequency information, data from these tows are not addressed in this paper.

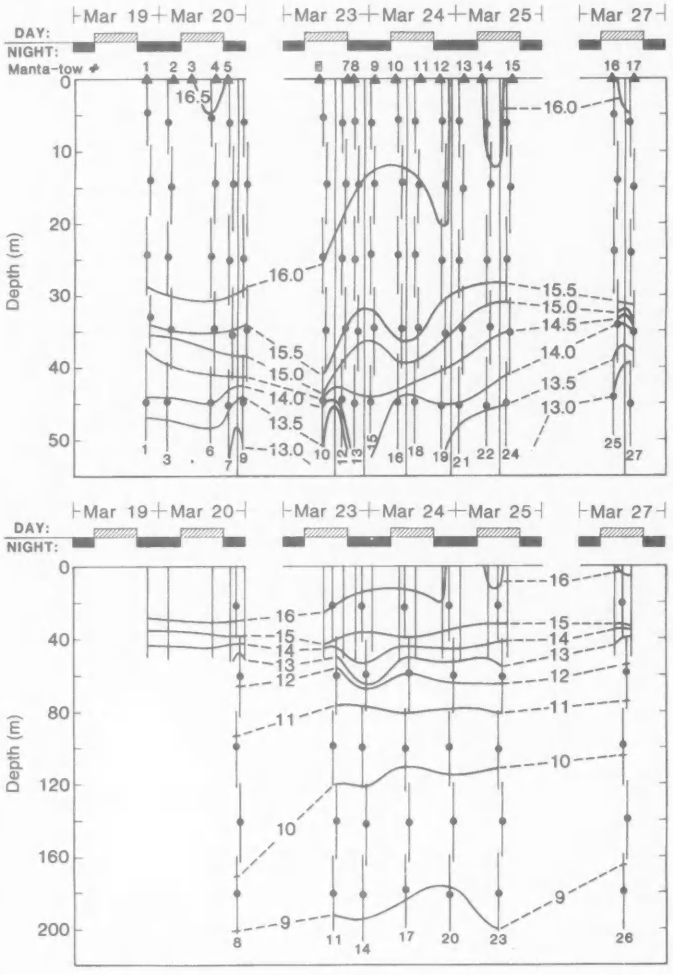

Figure 2

Diagram showing chronology of MESSHAI tows, depth strata sampled, and isotherms for the offshore station (from Pommeranz and Moser, 1987). (**Above**) Shallow (50 m) and Manta tows; the dots represent average depths for each net; the seven complete vertical lines show when deep (200 m) tows were taken. Tow numbers for Manta tows are given above solid triangles and tow numbers for MESSHAI tows are given at the bottom of each series of vertical lines. Isotherms are shown in 0.5°C intervals. (**Below**) Deep tows; the 17 lines extending down to 50 m indicate when shallow tows were taken. Isotherms are shown in 1°C intervals.

Most samples were preserved in 5% buffered formalin; selected samples were preserved in 80% ethyl alcohol for analysis of otolith daily growth rings in anchovy larvae. Prior to sorting, wet zooplankton displacement volume of each sample was measured using standard techniques (Kramer et al., 1972). Anchovy larvae and eggs were identified and removed during the plankton sorting process; eggs were classified by stage according to the criteria of Moser and Ahlstrom (1985) and length measurements of larvae were taken to the nearest 0.5 mm. Larvae of other fish were identified to the lowest taxon possible

and body lengths were measured to 0.1 mm.

We used analysis of variance (ANOVA) to compare the pre- and poststorm densities of anchovy eggs and larvae for shallow strata and also for deep strata at the inshore and offshore stations. Day and night data were pooled for each of these categories because the data did not indicate a diurnal shift in vertical distribution of eggs or larvae. All data were log-transformed for statistical analyses because the original data were highly skewed. Data from the shallow strata included the Manta tows, the MESSHAI shallow tows (0–50 m), and the upper 40 m from the MESSHAI deep tows. Data for the deep strata were from below 40 m from the deep MESSHAI tows. A two-way ANOVA was performed for the shallow strata, the two factors being station (inshore and offshore) and tow type (Manta, MESSHAI shallow, and MESSHAI deep). Interaction terms were included in the analysis. One-way ANOVA was performed for data from the deep strata to compare anchovy larval density at inshore and offshore stations.

In the analysis of prestorm and poststorm conditions two separate ANOVAs were performed because an initial ANOVA of anchovy eggs from the shallow strata indicated a strong interaction between tow type and pre- or poststorm period; one analysis was based on data from shallow and deep MESSHAI tows and the other was based on Manta tows only. A single two-way ANOVA test was performed for anchovy larvae because the density of anchovy larvae in Manta tows was low and the analysis adequately described the effect of the storm on larval density based on both shallow and deep MESSHAI tows.

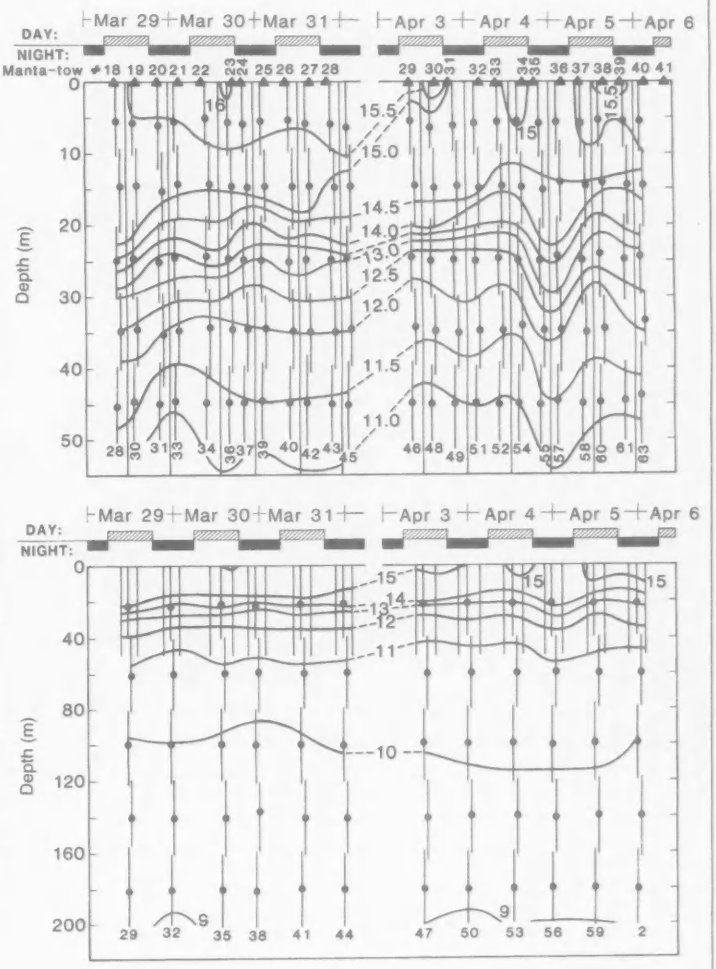

Figure 3

Diagram showing the chronology of MESSHAI tows, depth strata sampled, and isotherms at the inshore station. Symbols and labels are the same as those in Figure 2 (from Pommeranz and Moser, 1987).

Results

Environmental features

The thermal structure of the study area was typical for March–April in that region of the SCB, with a pool of relatively warm water subject to intrusions of advected upwelling plumes from the Point Conception area (Lasker et al., 1981; Lynn et al., 1982). The mixed layer was about 30–40 m deep at the offshore station (Fig. 2) and only about 10–30 m deep at the inshore station (Fig. 3). Overall, the water was colder at the inshore station, which lacked the prominent 16.0° isotherm present offshore. Average temperature was higher at the offshore station in all depth strata except 160–200 m (Fig. 4, A and B). At the inshore station after the storm the thermocline shoaled to 15–20 m and water temperature was lower

than before the storm at all depths below 80 m (Figs. 2; 3; 4, C and D).

Wind and sea-state observations taken during the cruise and supplemented by data from the Naval Air Station at San Clemente Island, southwest of the offshore station, and the San Onofre Nuclear Generating Station, just southeast of the inshore study area (Fig. 1), indicated an oscillating land-sea system which was more evident at San Onofre than at San Clemente (Fig. 5). During the night and morning, winds typically were from the NNE, after which they shifted through the south to the NW until late afternoon or evening. Average wind speed was about 10 knots at the offshore station and about 6 knots at the inshore station; average swell height was about 1.7 m and about 1 m at the two sites, respectively (Fig. 6). At the inshore station wind speed was more than 24 knots during the storm.

Prior to the storm at the inshore station there was a moderate to strong chlorophyll maximum at 18–29 m (Fig. 7). Following the storm, the chlorophyll peak became shallower and generally broader. The peak was at 15 m on the morning of 3 April; by the evening of 4 April, the maximum was near the surface. On the following two days the peak reappeared and began to deepen and strengthen. Average plankton volumes of Manta and MESSHAI samples from the upper 40 m were distinctly higher at the inshore station than at the offshore station (Fig. 8, A and B). Average volumes were generally higher in strata within the upper 40 m in poststorm samples compared with those taken prior to the storm (Fig. 8, C and E). Average plankton volume increased markedly in the 40–80 m stratum, whereas there was little change in deeper strata (Fig. 8E).

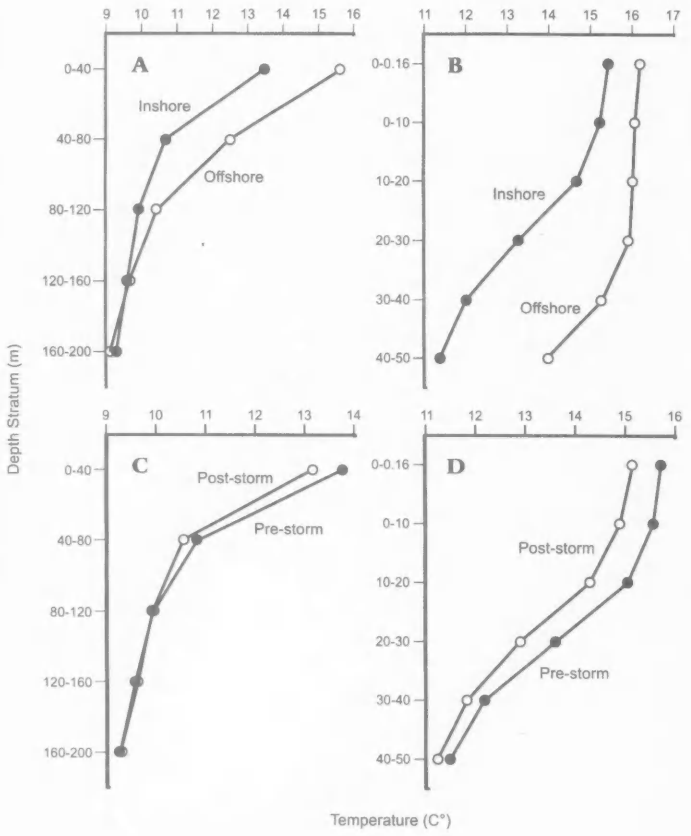

Figure 4

Average temperatures for strata sampled with the MESSHAI, based on data from the MESSHAI temperature sensor. (**A**) Deep tows at inshore (dots) and offshore (circles) stations; (**B**) shallow tows at inshore (dots) and offshore (circles) stations; (**C**) deep tows at inshore station before the storm (dots) and after the storm (circles); (**D**) shallow tows at inshore station before the storm (dots) and after the storm (circles).

Engraulis mordax eggs

A total of 67,157 *E. mordax* eggs were collected in the MESSHAI and Manta nets. Anchovy eggs had a slightly shallower distribution than larvae, with approximately 95% of eggs in the upper 30 m (Fig. 9, A and B). In shallow strata (including Manta, shallow MESSHAI, and the 0–40 m stratum of the deep MESSHAI tows), average density was greater at the offshore station than at the inshore station ($F_{1,95}$=4.72, P=0.003). Yet egg density in the deep strata was similar at the two stations. Average egg density in the surface layer was more than double that in the 0–10 m stratum (Fig. 9B). In the shallow strata at the inshore station, egg densities in MESSHAI tows were reduced after the storm ($F_{1,32}$=12.73, P=0.001), whereas egg densities did not change much in Manta tows ($F_{1,22}$=1.58, P=0.048) and in deep (>40 m) MESSHAI tows ($F_{1,10}$=2.67, P= 0.132) (Fig. 9, C and F).

Fish larvae

A total of 95,552 fish larvae were taken in the MESSHAI and Manta nets,

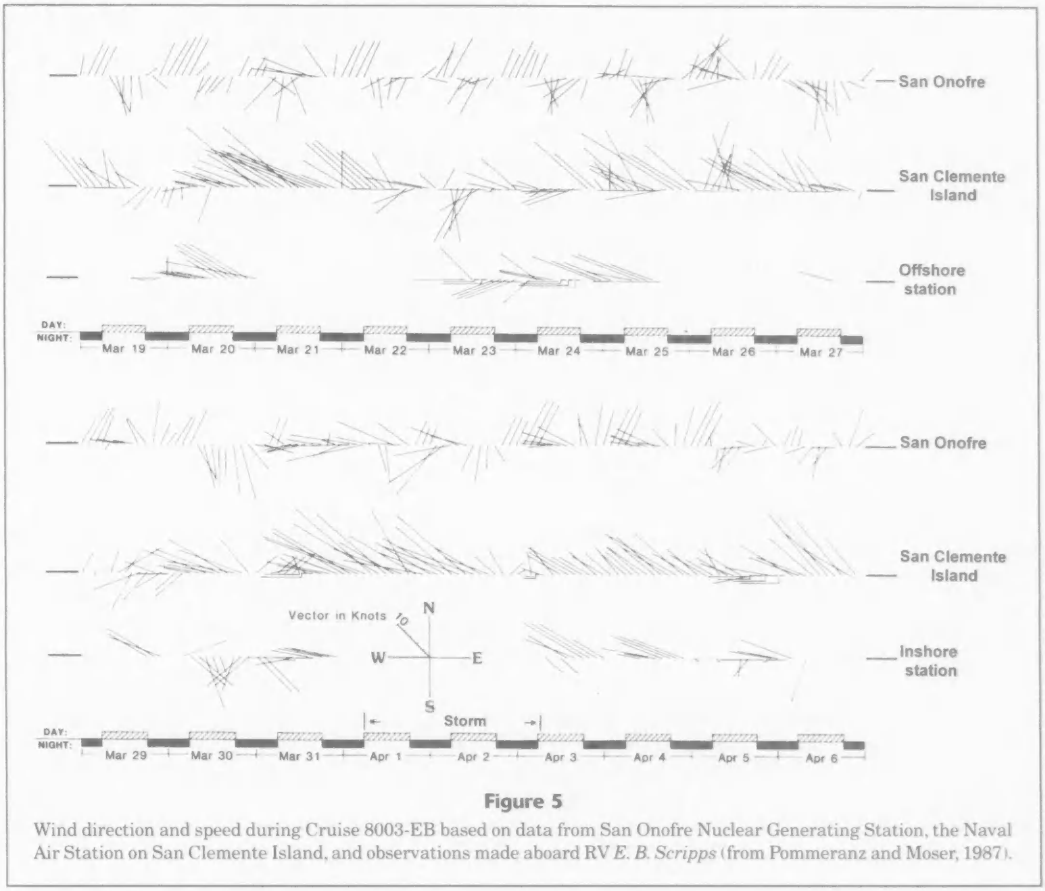

Figure 5

Wind direction and speed during Cruise 8003-EB based on data from San Onofre Nuclear Generating Station, the Naval Air Station on San Clemente Island, and observations made aboard RV *E. B. Scripps* (from Pommeranz and Moser, 1987).

representing 49 taxa (genera or species) in 27 families; 90,402 (95% of the total) were northern anchovy, *Engraulis mordax* (Table 1). Anchovy larvae were more than 40 times as abundant as the next most abundant species, California smoothtongue (*Leuroglossus stilbius*). White croaker (*Genyonemus lineatus*) ranked third, and the northern lampfish (*Stenobrachius leucopsarus*) ranked fourth, followed by the rockfish genus *Sebastes*. These five taxa constituted 99% of the total larvae. Following in abundance were queenfish (*Seriphus politus*), Pacific pompano (*Peprilus simillimus*), California halibut (*Paralichthys californicus*), the sanddab genus *Citharichthys*, and Pacific hake (*Merluccius productus*) (Table 1).

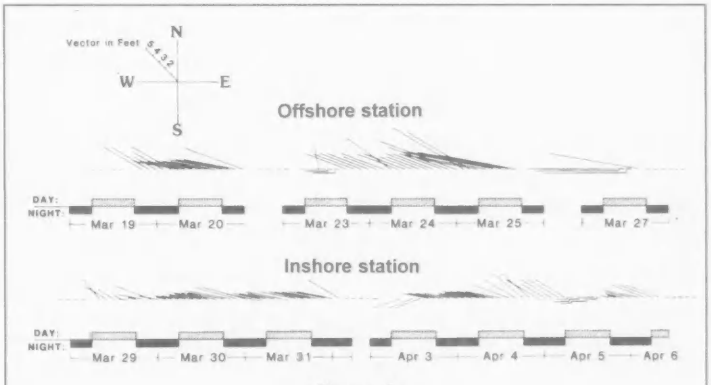

Figure 6

Swell direction and height during Cruise 8003-EB from observations made aboard RV *E. B. Scripps* (from Pommeranz and Moser, 1986).

Most of the larvae captured in the MESSHAI nets were at yolksac and preflexion stages. Relatively fewer anchovy larvae <3.0 mm and relatively more anchovy larvae >3.0 mm were taken by the bongo

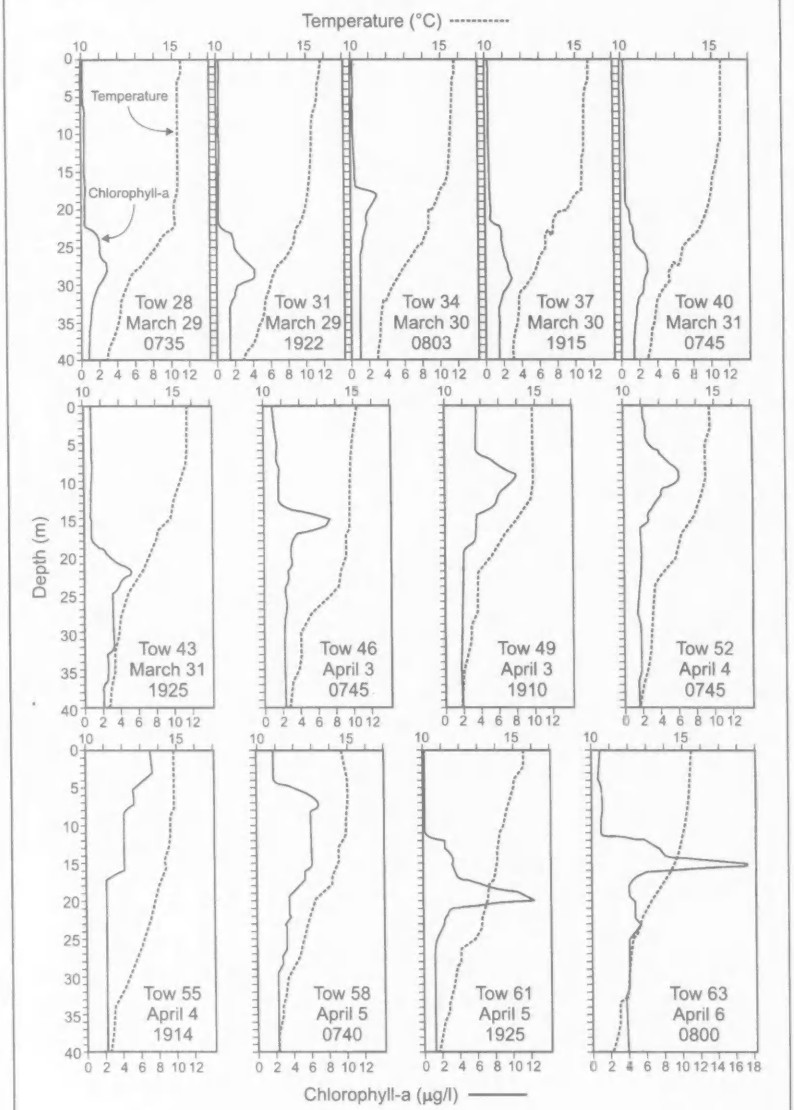

Figure 7

Chlorophyll-*a* (µg/l) and temperature (°C) profiles at the inshore station on Cruise 8003-EB. Tow numbers are given for shallow MESSHAI tows from which temperature profiles were derived.

net than in the MESSHAI tows (Fig. 10, A and B). The length-frequency distribution of larvae captured by the Manta net was bimodal, with peaks at 3.0 and 7.0 mm (Fig. 10C). For species other than northern anchovy, length distributions generally were similar for larvae caught in Manta and MESSHAI nets. Exceptions were a sample of 38 *Sebastes* spp. larvae captured in Manta net tow 18 (length range 5.0–9.4 mm, average length 7.2 mm) and an 8.0 mm presettlement *Paralichthys californicus* larva captured in Manta tow 31.

***Engraulis mordax* larvae** Anchovy larvae had a shallow distribution, with approximately 90% of the larvae in the upper 30 m (Fig. 11, A and B). In shallow strata, average larval density was greater at the

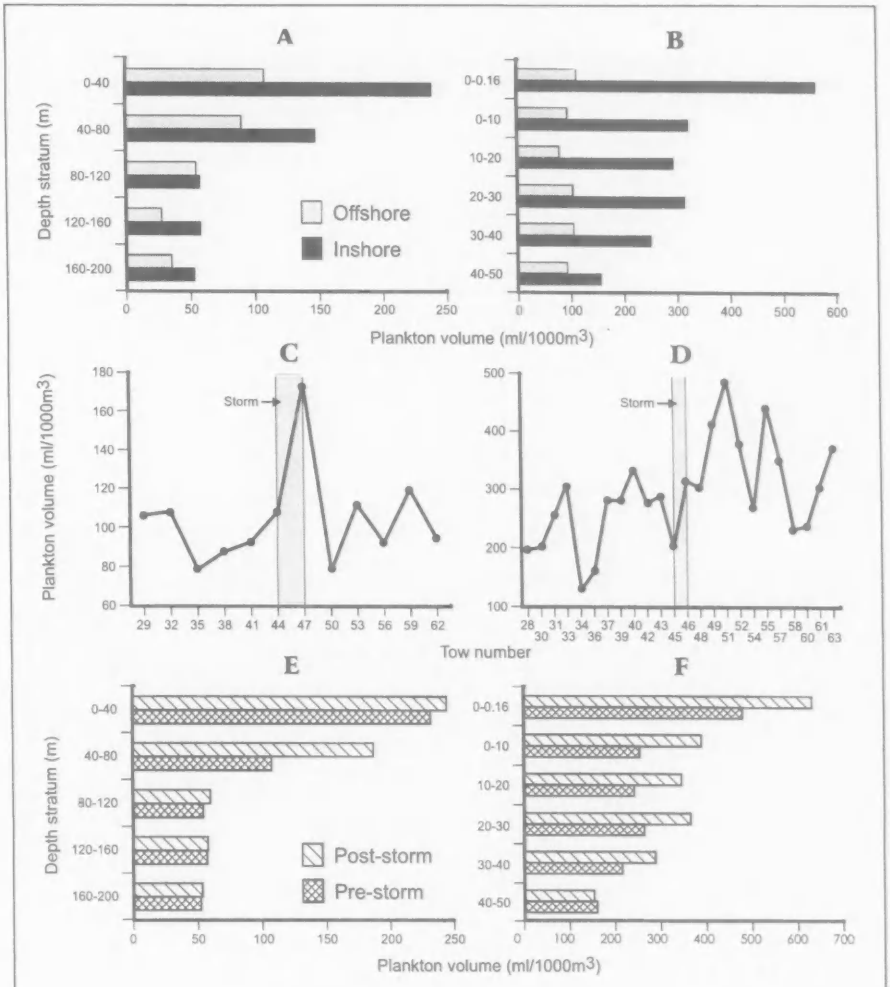

Figure 8

Plankton volumes (mL/1000 m³) in MESSHAI tows. Average volumes from (**A**) deep tows and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) volumes in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) volumes in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep tows and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

inshore station than at the offshore station (Fig. 11A; ANOVA of shallow strata, $F_{1,95}$=31.78, P=0.003). Within the upper 50 m at the inshore station, average density was highest in the 10–20 m stratum, accounting for approximately 40% of larvae. Density in the surface layer was comparatively low. In deep strata no significant difference in larval density was found between inshore and offshore stations ($F_{1,17}$=0.53, P=0.47). At the inshore station, average larval densities were lower in poststorm samples than in prestorm samples (shallow strata: $F_{1,54}$= 11.21, P=0.001; deep strata: $F_{1,10}$=10.05, P=0.001). Overall, larval distribution was somewhat shallower after the storm (Fig. 11, E and F).

***Leuroglossus stilbius* larvae** In deep MESSHAI tows, larvae of *L. stilbius* occurred in relatively high densities in most strata down to 200 m (Fig. 12A). The lower limit of their distribution was not determined by the MESSHAI samples, but another study

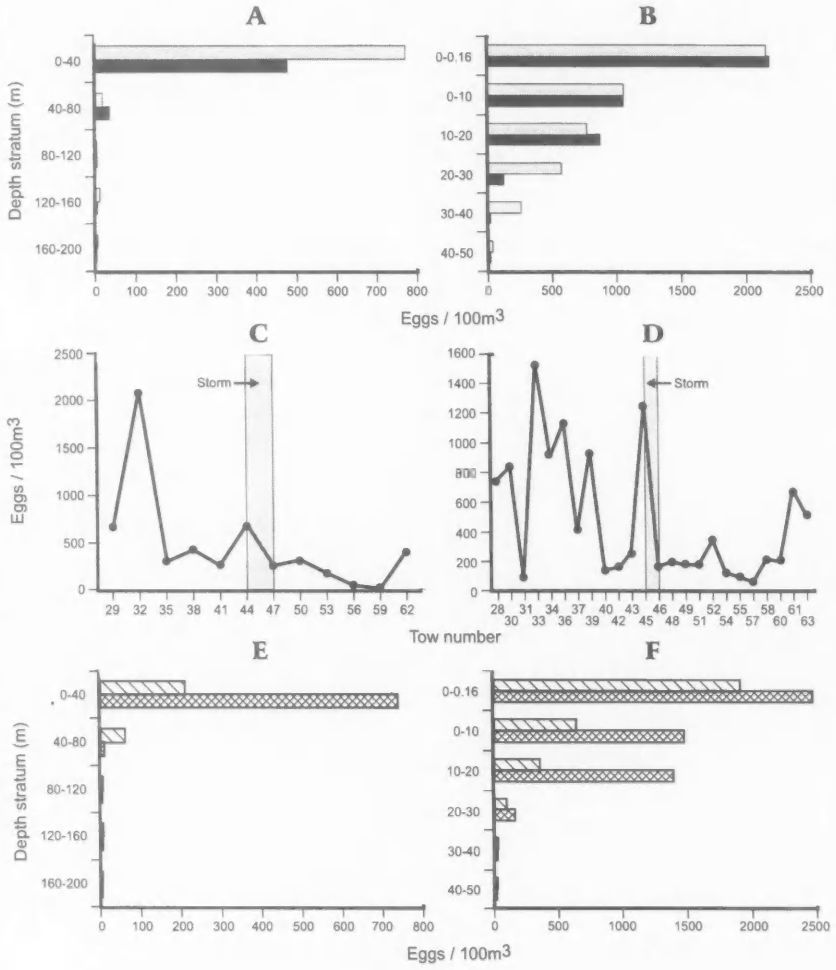

Figure 9

Anchovy eggs (no./100 m³) in MESSHAI tows. Average from (**A**) deep tows and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep tows and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

(Moser and Smith, 1993) showed that they may occur down to 300 m. Average densities were generally higher at the inshore station than at the offshore station. Larvae were absent from the 0–40 m stratum offshore and were nearly absent from this stratum in prestorm inshore samples (Fig. 12, A and E). In samples at the inshore station, average densities following the storm increased markedly at 0–80 m, decreased at 80–160 m, and increased slightly in the 160–200 m stratum (Fig. 12E). Larvae were not taken in Manta tows nor in the upper 40 m of shallow MESSHAI tows at the offshore station (Fig. 12B). At the inshore station the distribution was shifted upward in poststorm samples and average larval densities were relatively high in strata as shallow as 30–40 m (Fig. 12F).

***Genyonemus lineatus* larvae** White croaker larvae were absent from offshore samples and were abundant only in the upper 30 m at the inshore station (Fig. 13, A and B). Average densities were extremely low in prestorm samples but were relatively high in

Table 1

Taxa captured by Manta and MESSHAI nets on Cruise 8003-EB. Numbers of larvae are unadjusted counts; occurrences are listed in parentheses with onshore occurrences to the left of the slash and offshore occurrences to the right. Only taxa identified to genus or species are included.

		Number of larvae and occurrences			
Taxon	Family	Manta	Shallow MESSHAI	Deep MESSHAI	Total
Engraulis mordax	Engraulidae	3,066 (24/15)	67,640 (24/17)	19,696 (12/7)	90,402 (99)
Leuroglossus stilbius	Bathylagidae	0	785 (22/2)	1,401 (12/7)	2,186 (43)
Genyonemus lineatus	Sciaenidae	49 (7/0)	740 (19/0)	173 (8/0)	962 (34)
Stenobrachius leucopsarus	Myctophidae	1 (0/1)	349 (24/9)	193 (12/7)	542 (53)
Sebastes spp.	Sebastidae	53 (3/0)	264 (22/12)	134 (10/7)	441 (54)
Seriphus politus	Sciaenidae	17 (6/0)	164 (12/0)	106 (5/0)	287 (23)
Peprilus simillimus	Stromateidae	6 (4/0)	180 (21/2)	35 (10/0)	221 (37)
Paralichthys californicus	Paralichthyidae	9 (3/0)	82 (16/0)	23 (6/0)	114 (25)
Citharichthys spp.	Paralichthyidae	0	63 (17/1)	14 (7/1)	77 (26)
Merluccius productus	Merlucciidae	0	36 (15/0)	12 (5/4)	48 (24)
Atherinopsis californiensis	Atherinidae	44 (9/0)	0	0	44 (9)
Pleuronichthys verticalis	Pleuronectidae	1 (1/0)	25 (9/0)	8 (3/0)	34 (13)
Lyopsetta exilis	Pleuronectidae	0	27 (16/0)	5 (4/0)	32 (20)
Bathylagus ochotensis	Bathylagidae	0	21 (13/0)	10 (4/4)	31 (21)
Parophrys vetulus	Pleuronectidae	0	19 (9/0)	7 (5/0)	26 (14)
Cataetyx rubrirostris	Bythitidae	0	20 (12/0)	4 (3/0)	24 (15/0)
Argentina sialis	Argentinidae	0	9 (8/0)	8 (6/0)	17 (14)
Protomyctophum crockeri	Myctophidae	0	1 (1/0)	10 (4/4)	11 (9)
Argyropelecus spp.	Sternoptychidae	0	0	9 (4/0)	9 (4)
Pleuronichthys spp.	Pleuronectidae	0	6 (3/0)	3 (3/0)	9 (6)
Ophidion scrippsae	Ophidiidae	0	1 (1/0)	6 (3/0)	7 (4)
Atractoscion nobilis	Sciaenidae	0	6 (2/0)	0	6 (2)
Neoclinus stephensae	Chaenopsidae	6 (2/0)	0	0	6 (2)
Hypsoblennius spp.	Blenniidae	3 (2/0)	2 (2/0)	0	5 (4)
Pleuronichthys coenosus	Pleuronectidae	4 (3/1)	1 (1/0)	0	5 (5)
Coryphopterus nicholsii	Gobiidae	0	4 (3/0)	0	4 (3)
Scorpaenichthys marmoratus	Cottidae	4 (2/0)	0	0	4 (2)
Triphoturus mexicanus	Myctophidae	0	1 (1/0)	3 (2/0)	4 (3)
Bathylagus wesethi	Bathylagidae	0	3 (2/0)	0	3 (2)
Chauliodus macouni	Chauliodontidae	0	0	3 (2/1)	3 (3)
Hypsopsetta guttulata	Pleuronectidae	0	3 (3/0)	0	3 (3)
Lampanyctus spp.	Myctophidae	0	1 (1/0)	2 (1/1)	3 (3)
Oxyjulis californica	Labridae	0	3 (2/0)	0	3 (2)
Tarletonbeania crenularis	Myctophidae	0	2 (2/0)	1 (1/0)	3 (3)
Zaniolepis frenata	Hexagrammidae	0	2 (2/0)	1 (1/0)	3 (3)
Girella nigricans	Kyphosidae	0	2 (2/0)	0	2 (2)
Pleuronichthys ritteri	Pleuronectidae	0	2 (1/1)	0	2 (2)
Tactostoma macropus	Melanostomiidae	0	0	2 (1/0)	2 (1)
Bathylagus milleri	Bathylagidae	0	1 (1/0)	0	1 (1)
Brosmophysis marginata	Bythitidae	0	1 (1/0)	0	1 (1)
Chilara taylori	Ophidiidae	0	1 (0/1)	0	1 (1)
Cololabis saira	Scomberesocidae	1 (0/1)	0	0	1 (1)
Hypsoblennius gentilis	Blenniidae	1 (1/0)	0	0	1 (1)
Hypsoblennius jenkinsi	Blenniidae	1 (1/0)	0	0	1 (1)
Lampanyctus ritteri	Myctophidae	0	1 (0/1)	0	1 (1)
Melamphaes sp.	Melamphaidae	0	1 (1/0)	0	1 (1)
Scomber japonicus	Scombridae	0	1 (1/0)	0	1 (1)
Trachipterus altivelis	Trachipteridae	0	1 (1/0)	0	1 (1)
Typhlogobius californiensis	Gobiidae	1 (1/0)	0	0	1 (1)

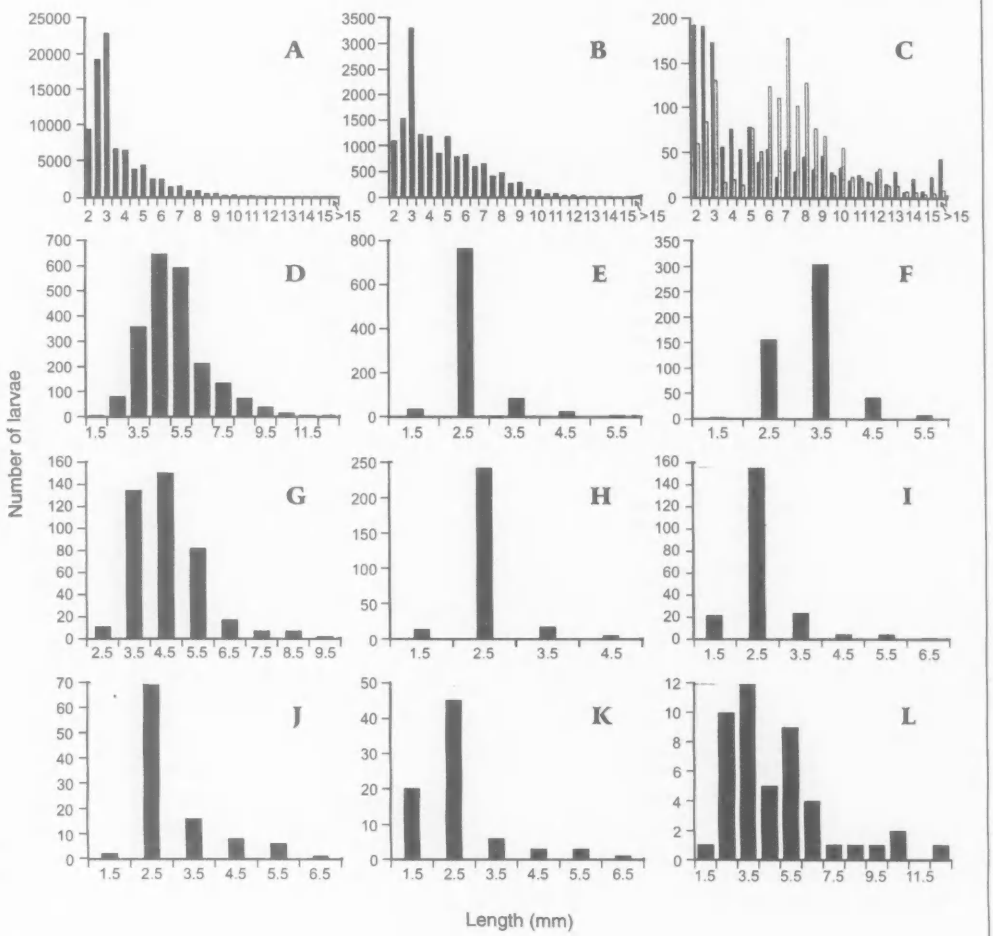

Figure 10

Length frequencies of larvae of the 10 most abundant taxa taken in MESSHAI (**A** and **D–L**), (**B**) oblique bongo, and (**C**) Manta tows on Cruise 8003-EB. (**A–C**) *Engraulis mordax*; day (shaded) and night (solid) are shown for Manta tows; (**D**) *Leuroglossus stilbius*; (**E**) *Genyonemus lineatus*; (**F**) *Stenobrachius leucopsarus*; (**G**) *Sebastes* spp.; (**H**) *Seriphus politus*; (**I**) *Peprilus simillimus*; (**J**) *Paralichthys californicus*; (**K**) *Citharichthys* spp.; (**L**) *Merluccius productus*. In A–C, bars represent 0.5-mm size classes; in D–L, bars represent the midpoints of 1.0-mm size classes.

poststorm samples from the surface to 30 m (Fig. 13, E and F). Individual tows showed a sharp increase in larval density immediately following the storm, peaking 2 days after the storm and declining to prestorm levels 3 days after the storm (Fig. 13, C and D).

***Stenobrachius leucopsarus* larvae** Larvae of northern lampfish occurred throughout the water column to 200 m depth at the inshore station, with highest average densities in the 20–30 m and 30–40 m strata (Fig. 14, A and B). Average densities were greater at the inshore station than at the offshore station. In deep MESSHAI tows taken at the offshore station, average density was greatest in the 40–80 m stratum; larvae were absent between 80 and 160 m. At the inshore station, maximum prestorm larval densities were in the 0–40 m and 40–80 m strata; in poststorm samples, densities were highest at 0–40 m (Fig. 14E). The center of distribution of larval densities from shallow MESSHAI tows shifted upward from 30–40 m in prestorm samples to 20–30 m in poststorm samples (Fig. 14F). Individual deep

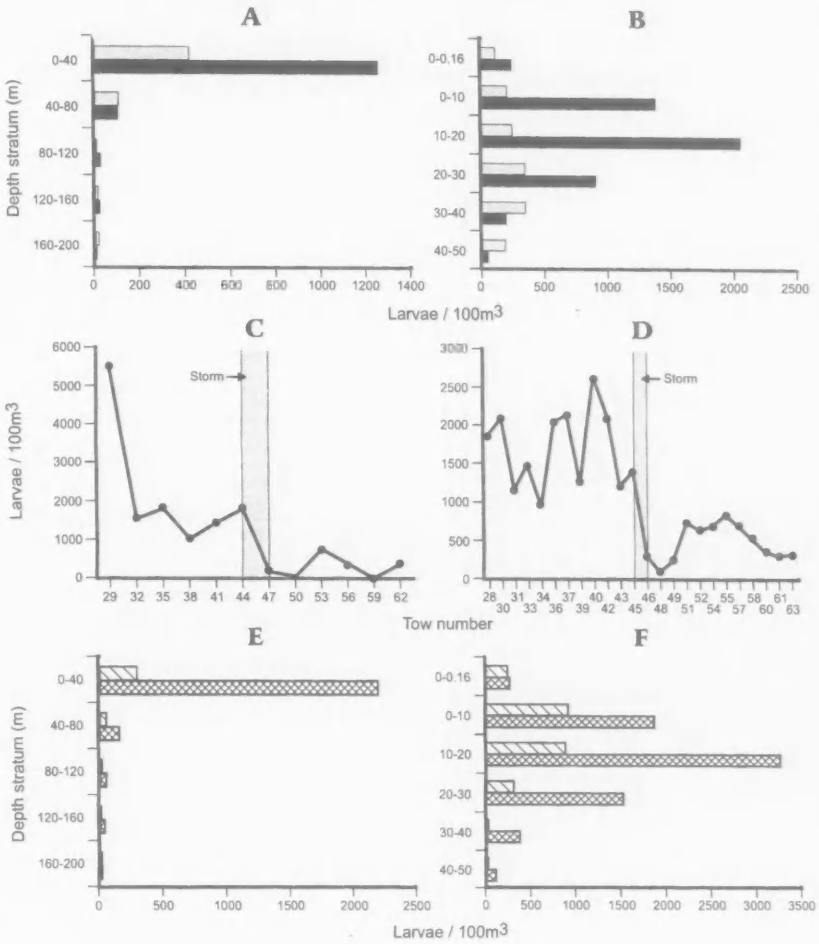

Figure 11

Anchovy larvae (no./100 m³) in MESSHAI tows. Average from (**A**) deep tows and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

MESSHAI tows in the upper 200 m showed a trend of increasing density just before the storm and a sharp decrease in poststorm tows (Fig. 14C). In shallow MESSHAI tows, densities peaked in two tows taken one day before the storm but were not appreciably different in pre- and poststorm samples (Fig. 14D).

***Sebastes* spp. larvae** Rockfish larvae were concentrated in the upper 80 m of the water column, with low average densities between 80 and 200 m (Fig. 15A). In deep MESSHAI tows the highest average density was in the 40–80 m stratum at the offshore station but in the 0–40 m stratum at the inshore station (Fig. 15A). In shallow MESSHAI tows at the inshore station, average density was highest in the 20–30 m stratum, relatively low in the 0–10 m and 10–20 m strata, and nearly as high at the surface as in the 20–30 m stratum. Offshore, shallow MESSHAI tows showed extremely low average densities in the upper 30 m of the water column; larvae were not taken in surface net tows. At the inshore station, average larval densities were higher in samples

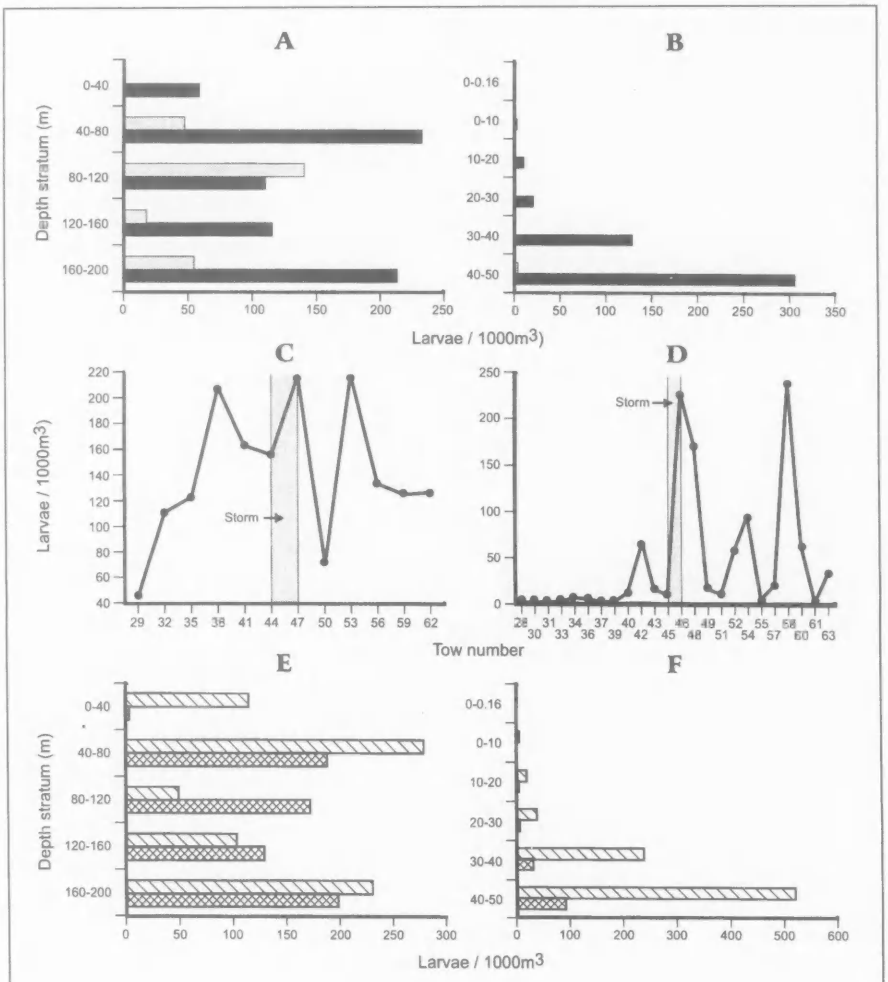

Figure 12

Leuroglossus stilbius larvae (no./1000 m³) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

taken before the storm than those taken afterwards; however, the disparity between average densities before and after the storm was due largely to several prestorm tows with unusually high larval counts (Fig. 15, C–F).

***Seriphus politus* larvae** Queenfish larvae occurred only at the inshore station, primarily in the upper 10 m of the water column (Fig. 16, A and B). At the inshore station, larvae were virtually absent from tows taken before the storm; larval density increased abruptly immediately following the storm, then subsided to prestorm level within about two days after the storm (Fig. 16, C–F).

***Peprilus simillimus* larvae** Larval Pacific pompano occurred primarily in the upper 40 m, with highest average densities in the upper 20 m of the water column (Fig. 17, A and B). Except for two tows at the 30–40 m stratum, larvae did not occur in offshore

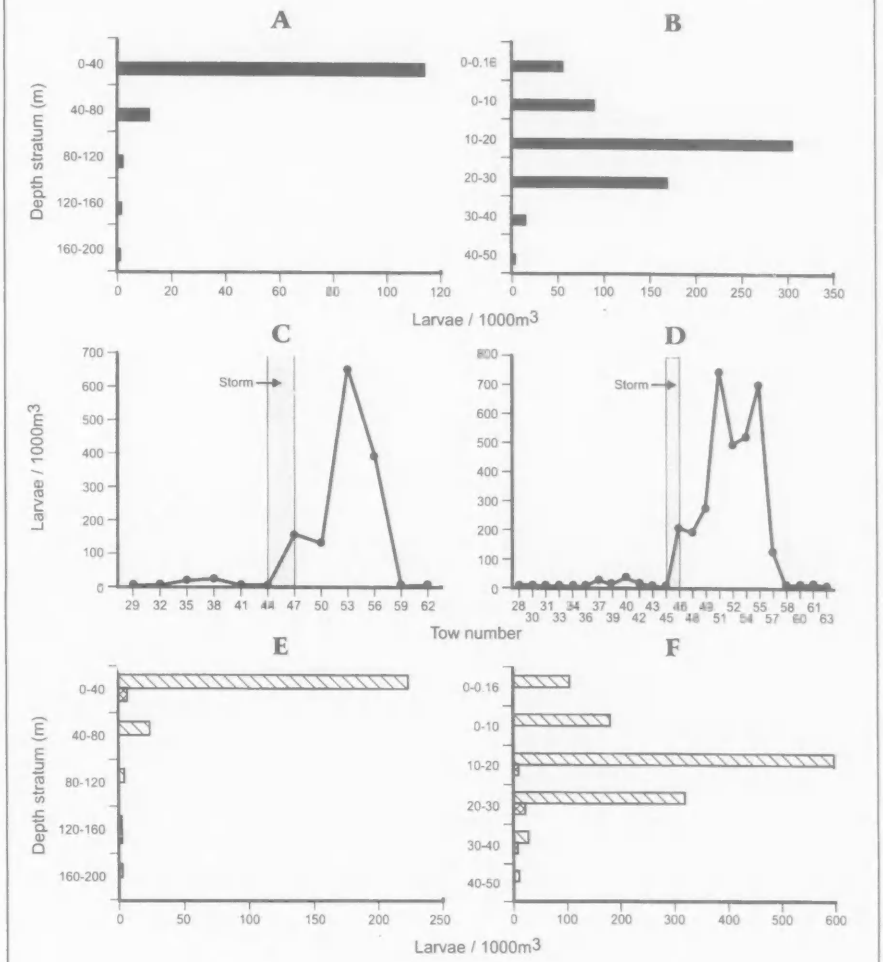

Figure 13

Genyonemus lineatus larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

samples. At the inshore station, larval densities were comparatively low in prestorm samples but increased markedly after the storm (Fig. 17, C–F).

***Paralichthys californicus* larvae** California halibut larvae occurred only at the inshore station and were restricted to the upper 30 m of the water column (Fig. 18, A and B). Average larval density was highest in the 0–10 m stratum, where it was four times higher than in the 20–30 m stratum or at the surface (Fig. 18B). Larvae appeared in several of the shallow MESSHAI tows prior to the storm at densities as high as approximately 20 per 1000 m^3; after the storm, densities increased steadily to more than 60 per 1000 m^3, then decreased to prestorm levels within 2 days following the storm (Fig. 18D). Average poststorm larval density for the 10-m stratum was more than 7 times higher than prestorm density, and overall vertical distribution was slightly shallower in poststorm samples (Fig. 18F). Larvae occurred in Manta net samples only in poststorm tows.

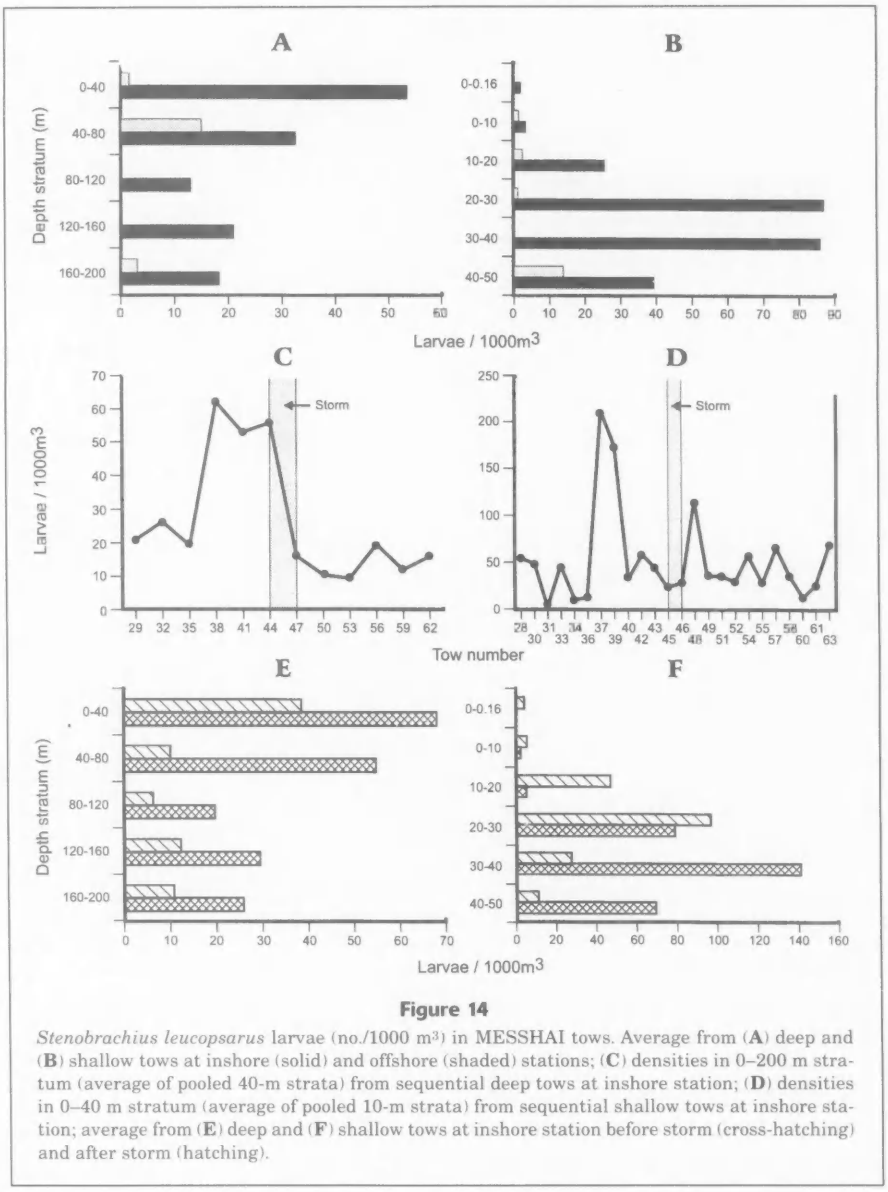

Figure 14

Stenobrachius leucopsarus larvae (no./1000 m³) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

***Citharichthys* spp. larvae** Sanddab larvae were taken primarily in the upper 50 m of the water column at the inshore station (Fig. 19, A and B). In shallow MESSHAI tows, peak average density was in the upper 10 m. Poststorm samples contributed most of the larvae (Fig. 19, C–F). A few larvae appeared sporadically in tows taken before the storm; following the storm there was a steady increase in larval density and then a sharp decline by the second day after the storm (Fig. 19, C and D). The distribution was shifted upward by approximately 20 m in poststorm samples (Fig. 19F).

***Merluccius productus* larvae** Hake larvae were taken in deep MESSHAI tows in the 40–80 and 80–120 m strata; average densities were similar in inshore and offshore samples (Fig. 20A). Larvae occurred in shallow MESSHAI tows only at the inshore station and were taken as shallow as 10–20 m (Fig. 20B). After the storm only one deep MESSHAI tow was positive, but for shal-

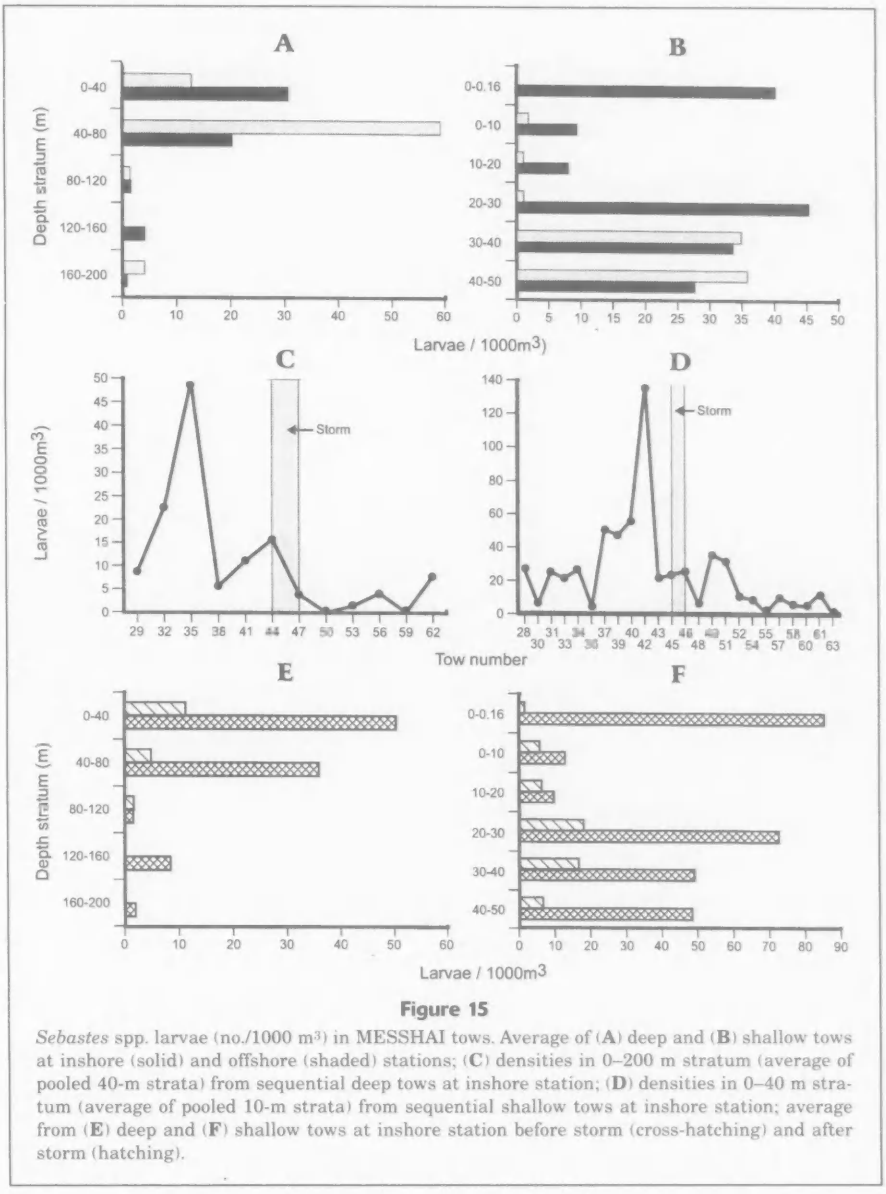

Figure 15

Sebastes spp. larvae (no./1000 m³) in MESSHAI tows. Average of (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

low MESSHAI tows, the frequency of positive tows increased, along with larval densities (Fig. 20, C and D). The distribution of larvae became somewhat shallower in shallow MESSHAI tows after the storm (Fig. 20F).

Discussion

Northern anchovy larvae dominated samples from both study sites. The midwater species *Leuroglossus stilbius* and *Stenobrachius leucopsarus* and the rockfish genus *Sebastes* were relatively abundant at the two sites. These three taxa, along with *Merluccius productus* (ranked 10th in abundance) and *Bathylagus ochotensis* (ranked 13th), constitute a distinct larval recurrent group in the California Current region (Moser and Smith, 1993). These three taxa were also closely linked in other analyses of larval fish assemblages in the study region (Gruber et al., 1982; McGowen, 1993). *Sebastes* spp. and *Merluccius*

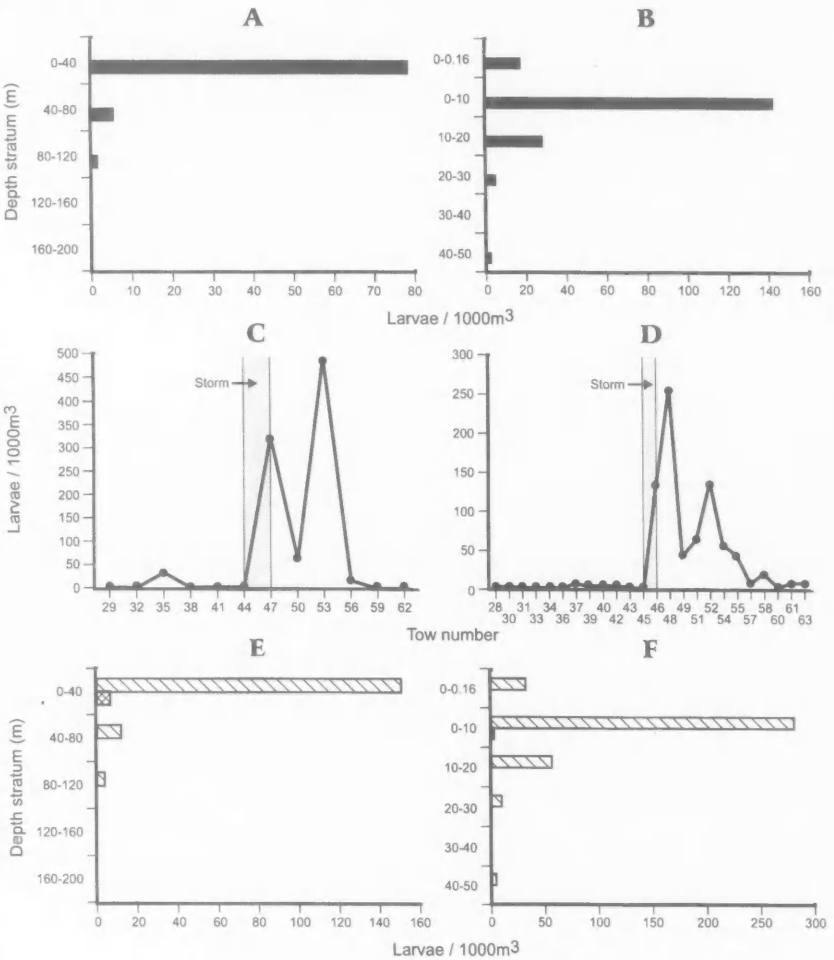

Figure 16

Seriphus politus larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

productus are demersal and their larvae are found throughout the SCB at this season (Moser et al., 1993). Other studies (Gruber et al., 1982; McGowen, 1993) have shown that larvae of *Leuroglossus stilbius* and *Stenobrachius leucopsarus* are relatively abundant nearshore and, according to Barnett et al. (1984), *S. leucopsarus* may extend shoreward to midshelf. This can be explained, in part, by the narrowness of the shelf in this region and the proximity to deep-water habitat. These species are unusual in comparison with other bathylagids and myctophids in this region in having relatively high larval abundances near the coast (Moser et al., 1993). Most larvae of other taxa collected in this study were taken at the nearshore station and represent demersal shelf species. The most abundant of these, *Genyonemus lineatus*, spawns during winter and early spring over shelf waters throughout the SCB (Gruber et al., 1982; Schlotterbeck and Connally, 1982; Watson, 1982; Barnett et al., 1984; Brewer and Kleppel, 1986; Lavenberg et al., 1986; Walker et al., 1987; McGowen, 1993; Moser et al., 1993). *Seriphus politus*, the next

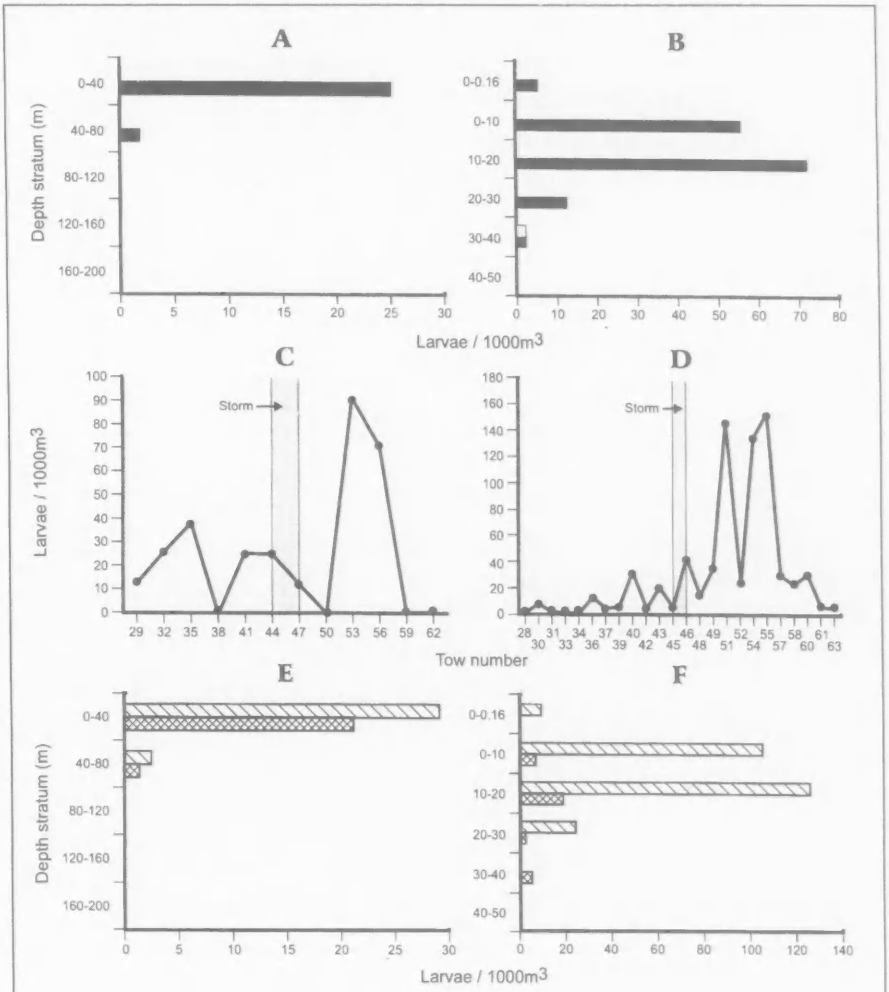

Figure 17

Peprilus simillimus larvae (no./1000 m³) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

most abundant shelf species in the samples, typically spawns from late spring to summer; however, spawning began unusually early in 1980 since larvae were abundant as early as March off San Onofre (Walker et al., 1987). *Peprilus simillimus*, *Paralichthys californicus*, and *Citharichthys* spp. have broad spawning seasons with high larval abundance in late winter to early spring. This was particularly evident in 1980 (Walker et al., 1987; Moser et al., 1993).

The vertical distribution of larval fishes is closely related to the temperature profile of the water column. Ahlstrom (1959) described two general categories: those taxa whose larvae occur almost entirely within the upper mixed layer and in the upper part of the thermocline; and those that occur within or below the thermocline. Larvae of shorefishes, including most clupeoids, typically fall within the first category. Generally, slope and offshore taxa produce deeper-living larvae, although many oceanic taxa also have shallow-living larvae. Northern anchovy had similar vertical profiles at the slope and offshore stations although densities were much higher at the slope station, where the

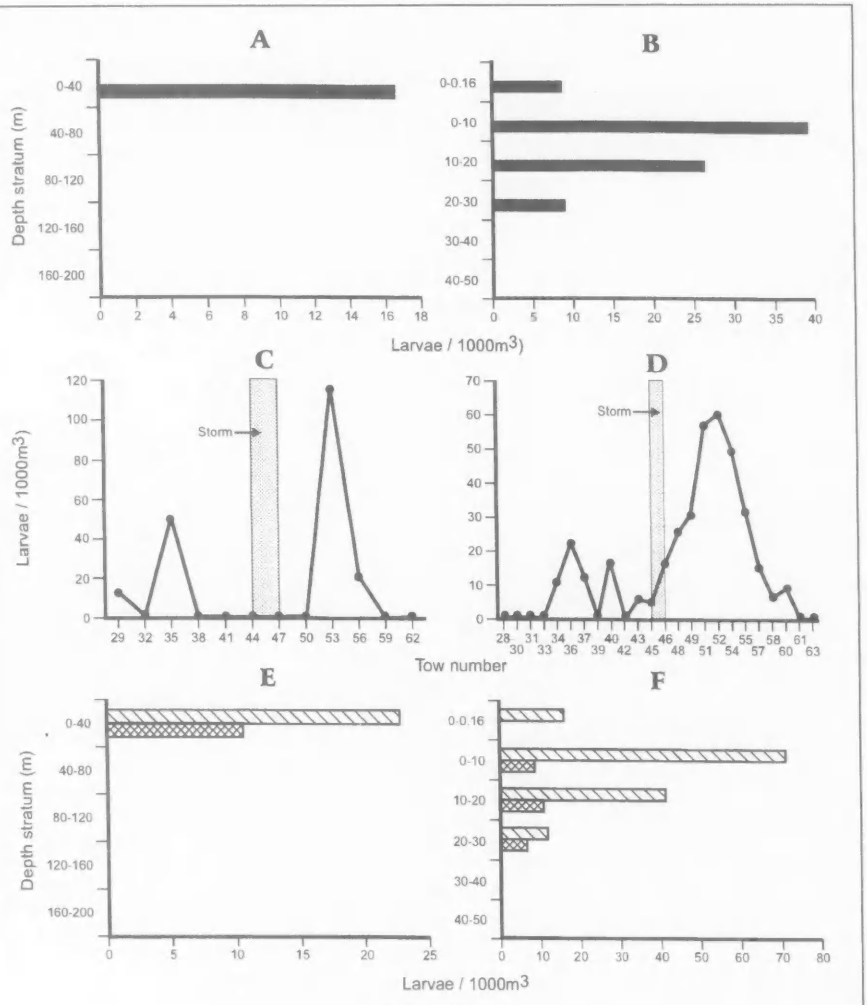

Figure 18

Paralichthys californicus larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–40 m stratum from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

density peak was more pronounced and was about 10 m shallower than at the offshore station. Probably this peak was related to the relatively shallow mixed layer at the slope station compared with the offshore station. Eggs of the anchovy had a shallower distribution than the larvae, with an apparent density peak in the neuston. The effect of the different mixed layer depths at the two stations is evident in the slightly deeper lower distribution boundary of eggs at the offshore station.

Like the anchovy, the nearshore shelf species (white croaker, queenfish, California halibut, California pompano, and some sanddab species) had shallow larval distributions essentially limited to the upper 30 m of the water column of the inshore station, with peak densities in either the 0–10 m or 10–20 m strata. Such shallow distributions appear to be typical of nearshore species although previous studies have lacked the fine-scale sampling capability needed to show this. The many *Sebastes* species occupy a wide range of habitats on the shelf and upper slope and produce larvae that are found within and below the thermocline and that generally avoid the upper mixed layer, except for the

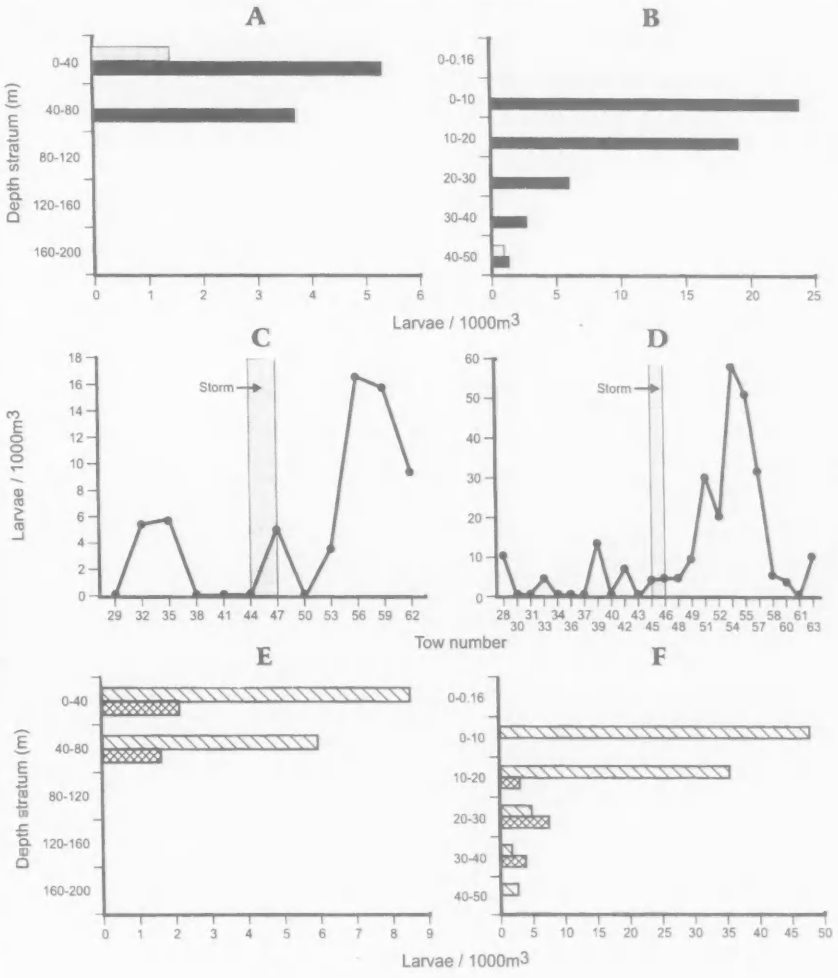

Figure 19

Citharichthys spp. larvae (no./1000 m³) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–80 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m strata (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

neustonic zone (Ahlstrom, 1959; Moser and Boehlert, 1991). This distribution is clearly shown by comparing the stratum of highest density at the inshore and offshore stations. Likewise, Pacific hake are broadly distributed over the shelf and slope and have deep-living larvae (Ahlstrom, 1959; Mullin and Cass-Calay, 1997). In our study, hake larvae were absent from samples above 50 m depth at the offshore station.

A comparison of larval anchovy length distributions from MESSHAI, bongo, and Manta net tows shows that the MESSHAI is less effective in catching larvae over 3 mm than the other two (Fig. 10, A–C). The mouth opening of the MESSHAI net is relatively much smaller (25×25 cm) than that of the bongo net (71 cm diameter). Why the Manta net captures larger larvae is conjectural. It may be related to the absence of an upward escape plane for larvae in the path of the net or it may reflect the size frequency of larvae in the surface layer. The bimodal length distribution for anchovy captured in Manta

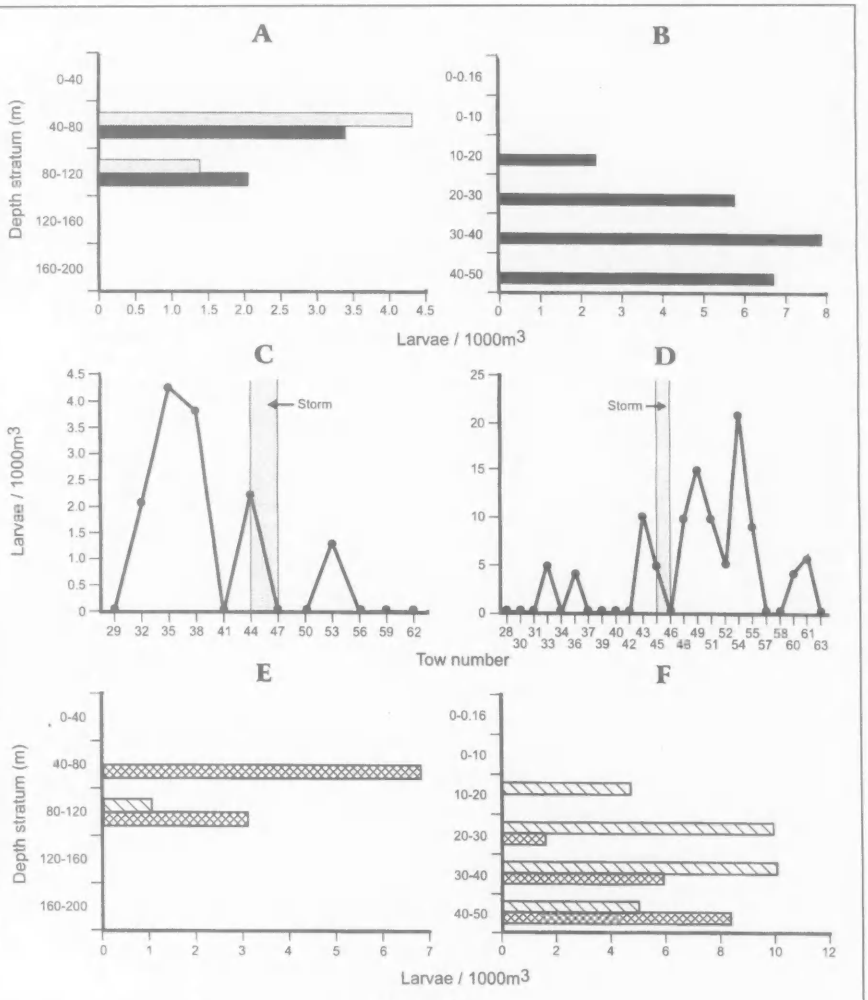

Figure 20

Merluccius productus larvae (no./1000 m^3) in MESSHAI tows. Average from (**A**) deep and (**B**) shallow tows at inshore (solid) and offshore (shaded) stations; (**C**) densities in 0–200 m stratum (average of pooled 40-m strata) from sequential deep tows at inshore station; (**D**) densities in 0–40 m stratum (average of pooled 10-m strata) from sequential shallow tows at inshore station; average from (**E**) deep and (**F**) shallow tows at inshore station before storm (cross-hatching) and after storm (hatching).

tows results from relatively large numbers of 6.0–10.0 mm larvae caught at the surface during the day (Fig. 10C). This was a consistent feature of Manta catches throughout the cruise, suggesting that anchovy larvae may have been migrating to the surface layer to feed during the day.

The storm that interrupted sampling for two days at the inshore station significantly affected the relative abundance and distribution of fish larvae and their physical and biotic environment. Average densities of anchovy larvae declined markedly in most strata following the storm, possibly as a result of mortality associated with starvation. This argument is contradicted by the results of Mullin et al. (1985) who showed that important larval fish prey, such as copepod nauplii increased in concentration after the storm, were no less stratified than before the storm, and had a 15-m upward shift in peak abundance that mirrored the shoaling of anchovy larval distribution in our study. Moreover, the chlorophyll maximum was

below the peak depth zone of anchovy larval abundance before the storm, whereas it coincided with the depth zone of highest larval abundance afterwards. Pre- and poststorm peak concentrations of important fish larva prey coincided with pre- and poststorm peaks in the chlorophyll maximum (Mullin et al., 1985). If starvation was the reason for the decline in anchovy larvae, then it is likely that the cause was disruption of micropatches of food, as suggested by Mullin et al. (1985). In this case, Lasker's (1981) stable ocean hypothesis was operative at the centimeter scale, and reduced survival was a result of disruption of the fine-scale geometry of food patches (Vlymen, 1977; Owen, 1989). Another explanation for the poststorm decline in anchovy larval abundance would be advection of larvae away from the study site (Mullin et al., 1985). The strong northwest winds resulted in offshore movement of surface water (the upper 10 m) by Ekman transport at a rate of about 10 cm per second; thus, virtually all the surface water at this region of the shelf was moved offshore during the storm and was replaced by deeper water (Winant[1]). This could explain the sharp decline in anchovy larval densities at the slope station after the storm, providing, of course, that densities of anchovy larvae were lower over the shelf than at the station before the storm. The latter would not be expected since Barnett et al. (1984) showed high concentrations of anchovy larvae over the shelf at a similar habitat south of our inshore station.

The storm had an opposite effect on densities of shorefish larvae (*Genyonemus lineatus, Seriphus politus, Peprilus simillimus, Paralichthys californicus, Citharichthys* spp.), which occurred in extremely low densities or which were absent in prestorm samples. Larval densities of these species began to increase immediately after the storm, peaked within 1–2 days, and then declined abruptly to prestorm levels. The sudden appearance of these larvae at the nearshore station after the storm was a result of storm-induced advection from shallow regions of the shelf. The narrow shelf in this region of the coast would make nearshore fish larvae particularly vulnerable to transport off the shelf during storms with northwest winds. Such advection may be important in the transport of nearshore fish larvae seaward where they become available to slope or eddy circulation, thus providing the opportunity for dispersion to other regions. The subsequent rapid decline in larval densities could have been caused by mortality associated with disturbance of micropatches of food, by predation, or by active or passive movement of larvae away from the sampling site. Starvation of these inshore larvae over slope waters may be related to the difference in composition and concentration of prey organisms in nearshore and offshore waters (Watson and Davis, 1989). Some portion of the larvae that appeared at the inshore site after the storm may have been transported back to the nearshore region. This return transport may have been enhanced by upward movement of these larvae to the surface where they could be carried by shoreward currents created by internal wave cells (Shanks, 1983, 1986).

Among the species with deeper-living larvae, those of *Sebastes* spp. declined markedly in all strata after the storm, whereas those of *Stenobrachius leucopsarus* showed a decline in deeper strata but increased in strata shallower than 30 m. This probably was caused by upward turbulent advection of larvae from deeper strata. Likewise, larval density of *Leuroglossus stilbius* increased in strata shallower than 50 m following the storm, with sporadic high counts in individual tows, suggesting pulses of upwardly advected larvae.

[1] C. D. Winant. 1998. Center for Coastal Studies, Scripps Institution of Oceanography, La Jolla, CA 92093. Personal commun.

Acknowledgments

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proved the manuscript. This paper is dedicated to the memory of our friend and mentor, Reuben Lasker, who wholeheartedly supported this study and provided encouragement and guidance to all of us.

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Growth of the tiger shark, *Galeocerdo cuvier*, in the western North Atlantic based on tag returns and length frequencies; and a note on the effects of tagging

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Abstract.—Growth parameter estimates were calculated for the tiger shark (*Galeocerdo cuvier*) by using tag and recapture data. Results were compared to published estimates based on bands in vertebrae. The von Bertalanffy parameters (sexes combined) based on tag and recapture growth data were as follows: L_∞ = 337 cm fork length, k = 0.178, and t_0 = −1.12. Monthly length-frequency data for six year classes from birth to two years old for tiger sharks were used to verify the tag-recapture growth curve for this age range. The predicted age at maturity is 7 years for both sexes. Data from an ongoing *in situ* study with oxytetracycline were used in conjunction with length data to determine the effect of tagging and oxytetracycline injection on growth. The data suggest that tagging alone or tagging combined with oxytetracycline injection has little or no effect on the growth rate of tiger sharks up to two years of age.

Adult tiger sharks, *Galeocerdo cuvier*, occur worldwide in temperate and tropical coastal waters. In the North Atlantic, they reside year round off the coast of Florida and seasonally migrate north as far as Nova Scotia, Canada (Kohler et al., 1995). Additionally, tiger sharks are known to make extensive migrations throughout the North Atlantic, on occasion traveling to Cuba and Africa.[1] The tiger shark is listed under the large coastal shark category of the Fisheries Management Plan for Sharks of the Atlantic Ocean (Anonymous, 1993). Although it is not a target species of the U.S. inshore longline fishery, small tiger sharks are frequently caught and released alive. Tagging and fishery data indicate that there is a nursery ground for tiger sharks on the continental shelf off the southeast coast of the US.[1] This area extends from about Augusta, GA, to Daytona, FL, and extends from shore seaward to depths of 100 m. A similar area exists off the coast of North Carolina.[2] In these areas, tiger sharks of birth size ranging from 61 cm fork length [FL]) to 120 cm FL are commonly caught in the commercial longline fishery. In the Northwest Atlantic, tiger sharks mature between 258 and 265 cm FL (Branstetter et al., 1987) and have been reported to attain a size of 469 cm FL (Castro, 1983).

Branstetter et al. (1987) used the alternating opaque and translucent bands formed in the vertebral centra to age tiger sharks caught in the western North Atlantic and the Gulf of Mexico. Attempts to verify these estimates with length-frequency analysis proved unsuccessful owing to the inability to distinguish age groups. Branstetter et al. (1987) tried to corroborate the vertebrally derived growth rate with results from one tag-recapture individual; however, this individual's length was estimated at both tagging and recapture. Owing to the high age estimates at L_∞, Branstetter et al. (1987) suggested that as tiger

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Fish. Bull. 97:944–953 (1999).

[1] 1992–98. Apex Predators Program, 28 Tarzwell Dr. Narragansett, RI 02882. NMFS unpub. data.

[2] Chris Jensen. 1994. Natl. Mar. Fish. Serv, NOAA, 28 Tarzwell Dr., Narragansett, RI 02882. Personal Commun.

sharks approach maximum sizes, their vertebrae and band deposition may not reflect age. Because attempts at verification were unsuccessful, and direct validation was not possible, the determination of the tiger shark growth rate was not completely satisfied.

To determine if vertebral growth bands reflect age in older individuals and possibly to verify the estimates of Branstetter et al. (1987), we undertook a study with tag and recapture data to estimate, independently, von Bertalanffy parameters for the tiger shark. Verification of neonatal and juvenile growth rates was accomplished by using monthly length-frequency data obtained over a period of seven years. In addtion, data on growth of oxytetracycline (OTC)-injected tagged and released tiger sharks from an ongoing study were available to compare with length-frequency and tagging growth data.

Figure 1

Map showing the portion of the nursery area (shaded box) from which monthly length-frequency samples were obtained.

Materials and methods

Data from tiger sharks were obtained between 1963 and 1997 from research vessel cruises, sportfishing tournaments, and the commercial shark fishery from Cape Cod, MA, to the Florida east coast. Data for monthly length-frequency analyses were obtained from tiger sharks caught by longline in a delineated area within the nursery grounds off Florida during 1988–94 (Fig. 1).

Length measurements

Measurements of total length (TL) and FL were taken to the nearest centimeter (cm) following the conventions of Bigelow and Schroeder (1948). Fork lengths are reported unless otherwise noted. TL to FL conversions can be calculated from the relationship

$$FL = (TL \times 0.8761) - 13.3535 \qquad r^2 = 0.99\ n{=}44$$

(Kohler et al., 1995)

Tag-recapture data

During 1962–96, over 6000 tiger sharks were tagged with NMFS tags (Casey, 1985) and released as part of the NMFS Cooperative Shark Tagging Program. Tags were returned primarily by sport and commercial fishermen who also reported shark size in TL, FL, or weight. All measurements and estimates were converted to FL.

Gulland and Holt's (1959) and Fabens' (1965) methods were used to calculate von Bertalanffy (1938) growth parameters from the tag-recapture data. Techniques for calculating the parameters according to Gulland and Holt (1959) came primarily from their publication and additional clarification was obtained from Cailliet et al. (1992). Only fish that were measured at both release and recapture and at liberty for at least 0.9 years were included in the analysis. Two of the three parameters for the von Bertalanffy (1938) growth function (VBGF), k and L_∞, were estimated directly with the methods of Fabens (1965) and Gulland and Holt (1959). T_0 cannot be estimated from tagging data alone, rather it requires an estimate of absolute size at age, such as size at birth, and was calculated with the VBGF and solving for t_0, such that

$$t_0 = t + (1/k)\left[\ln\left\{(L_\infty - L_t)/L_\infty\right\}\right],$$

where L_t = known length at age (size at birth);
k = the von Bertalanffy growth constant; and
L_∞ = the theoretical maximum attainable length from the VBGF.

The t_0 values were calculated based on an average size at birth of 61 cm FL[1] with $t = 0$.

Longevity was estimated from the FL at which >99% of the L_∞ was reached (i.e. $7\ln 2/k$) (Fabens, 1965; Cailliet et al., 1992). The von Bertalanffy parameters derived from these methods were compared with growth information obtained from the length-

frequency analysis. No OTC-injected individuals were included in these calculations.

Tag-recapture with OTC injection

During 1985–97, more than 650 tiger sharks (59 to 291 cm FL) were measured, injected with a 25 mg/kg body weight dose of OTC (Gruber and Stout, 1983), tagged, and released. To determine the effects of OTC on growth, data from recaptured OTC-injected fish were analyzed separately from those of noninjected recaptured fish. Only those OTC-injected specimens measured at both tagging and recapture and at liberty for at least 0.9 years were included in the analysis. For comparison of growth of injected fish to growth of noninjected fish, the growth rates from OTC-injected individuals were plotted with the von Bertalanffy growth function (VBGF) from the tag-recapture analysis. The size at tagging was used as a guide to estimate age at tagging with the VBGF. The time at liberty determined the distance along the x-axis, and sizes at recapture determined the slope. The growth of the OTC-injected individuals was then compared graphically with the growth curves for long-term (>0.9 yr) tag-recaptured sharks and monthly growth estimates.

Monthly growth

Data for tiger sharks measured and subsequently tagged from the defined nursery area were analyzed for monthly growth. Data on measured fish were available by month from June 1988 to August 1994. Data were organized into 5-cm intervals. The modes for the 1988, 1989, 1990, 1991, 1992, and 1993 year classes were followed progressively from the birth mode until the last visible mode for that year class. Where modes were not clear (i.e. single fish at more than one interval) the mean was taken as the mode. Previously tagged individuals were not included in this data set. Length-frequency histograms were developed for each month of each year for modal analysis. To determine if the data from the six year classes could be combined, the modes of each year class were plotted by month and compared graphically and through an analysis of covariance. Growth per year was calculated by subtracting the June birth mode from the June one-year mode and the June one-year mode from the June second-year mode. To compare the growth of these fish to tagged noninjected fish and tag-recaptured OTC-injected fish, month-per-year growth rates were plotted against the VBGF from the recapture analysis and the growth rates from the individual tag-recaptured OTC-injected fish. The initial positioning of the modes on the x-axis assumes birth takes place in June[1] so that the first point of the monthly growth was fixed on the monthly tag-recapture curve for June. The monthly growth values were fixed on the curve on the basis of month they were calculated for (i.e. June, birth; June, year 1; June, year 2). Graphical comparisons enabled us to determine whether growth based on the tag-recapture analysis was distinct from growth based on a method without tagging (represented by monthly growth). In addition, we compared Branstetter et al.'s (1987) vertebral growth curve to these data.

Results

Tag-recapture data

Information on 42 recaptured tiger sharks, measured at both tagging and recapture and at liberty for at least 0.9 years, was used to produce values of L_∞ and k of the VBGF (Table 1). The Gulland and Holt (1959) method produced the most biologically plausible estimates of VBGF parameters (Table 2). The Fabens (1965) analysis underestimated L_∞ with known maximum size estimates, and the value for k was high. Therefore, further analysis was based on the results from the method of Gulland and Holt (1959). Age at maturity, based on lengths at maturity from Branstetter et al. (1987), for female (265 cm FL) and male (258 cm FL) tiger sharks is 7 years (Fig. 2; Table 3). Maximum age was estimated to be 27.3 years (335+ cm FL > 99% of L_∞).

Tag-recapture with OTC injection

Analysis of the growth of the four OTC-injected specimens recaptured >0.9 years after tagging indicates that individuals grew at approximately the same rate as predicted by the tag-recapture data (Fig. 3). Growth calculated for the first year (growth/year of two individuals tagged at <100 cm FL) was 42.3 and 48.4 cm/yr. and 39.4 and 48.7 cm/yr. for the second year (growth/year two individuals tagged at >100 cm FL) (Table 1). These four individuals were at liberty between 0.94 and 1.19 years.

Monthly growth

Modes were clearly visible in the length-frequency histograms for small tiger sharks of all year classes from birth to 1.5 years. The modes for 1.5–2 years were less distinct owing to decreased sample sizes at the larger sizes (Fig. 4). Differences in growth rates among the six year classes were statistically significant (ANCOVA, P>0.05) so we did not combine the monthly length frequencies for all years (Fig. 4). In

the first year, the young grew from an average birth size of 65 cm FL to 100–105 cm FL with a growth rate of 40–45 cm/yr. (Fig. 4). More limited data on second year growth indicated a rate of 35–45 cm/yr. Even with this variation, growth in all years paralleled the tag-recapture growth curve and the individual growth rates of the OTC specimens (Fig. 3).

Discussion

It is evident that traditional methods for aging teleosts do not always work well for sharks. Length-frequency analysis is difficult owing to the slow growth exhibited by most elasmobranch species. Hard part analysis requires validation of the periodicity of band formation, which is often difficult to obtain for shark species. Vertebral age estimates for the sandbar shark, *Carcharhinus plumbeus*, which was one of the six species considered validated, have been revised since Cailliet's (1990) paper by using tag and recapture evidence (Casey and Natanson, 1992). The new data indicate that although the vertebral bands may be formed annually in the young shark, as validated (Branstetter, 1987b), they are not formed annually throughout the life of the shark and, therefore, band counts severely underestimate age. This type of revision highlights the need for validation of all size classes. It is advisable to use several methods for aging to provide verification for the chosen growth curve, particularly if vertebral band counts are used without direct validation.

Tag-recapture data can be a useful tool for age and growth determination if accurate measurements are taken at both tagging and recapture and if individuals are at liberty for a sufficient time for growth to occur. However, problems are associated with this method as well. For example, most length measurements are estimated by recreational and commercial fishermen. For slow growing sharks, it is imperative to obtain accurate length measurements, particularly in large fish. This can prove difficult as well as dangerous at tagging. Therefore, data on large individuals is sometimes lacking and thus will bias results. Additionally, some researchers have shown that tagging with "M" type tags in small sharks, such as the lemon shark, may retard growth (Manire and Gruber, 1991). Analysis of the data can also be problematic. The Fabens (1965) method can lead to biased estimates because its basic premise, that tagged individuals are at large for equal time periods, is often violated with sharks. Estimates from that method lead to low values of L_∞ and high values of k (Chien and Condrey, 1987). The Gulland and Holt (1959) method, which allows for unequal times at liberty,

Table 1

Tag-recapture data used for growth and growth rate analyses. TAL = time at liberty, FLTAG = fork length at tagging, FLCAP = fork length at recapture, b = value calculated from Gulland and Holt (1959). Also shown are the data for the OTC-injected recaptured fish, although they were not included in growth analyses.

Id No.	Sex	TAL (yr)	FLTAG (cm)	FLCAP (cm)	Average growth/yr (cm)	b
1	M	4.02	75.0	222.0	36.5	0.26
2	F	1.39	76.0	122.0	33.1	0.09
3	M	1.69	76.2	111.8	21.0	0.11
4	F	0.90	77.0	124.0	52.3	0.06
5	F	1.42	78.7	114.3	25.1	0.09
6	F	1.75	79.0	136.0	32.5	0.12
7	M	0.97	85.0	130.0	46.6	0.06
8	F	1.60	86.0	171.0	53.0	0.11
9	F	1.22	88.0	128.0	32.8	0.08
10	F	0.91	89.0	120.0	34.0	0.06
11	F	0.92	90.0	155.0	70.9	0.06
12	F	4.90	91.0	211.0	24.5	0.32
13	M	1.00	91.0	122.0	30.9	0.07
14	F	4.90	91.0	211.0	24.5	0.32
15	M	2.04	91.0	168.0	37.7	0.13
16	F	1.03	94.0	136.5	41.2	0.07
17	F	1.60	96.0	157.0	38.1	0.11
18	M	1.01	97.0	147.0	49.5	0.07
19	F	1.51	98.0	154.0	37.0	0.10
20	M	0.97	98.0	142.0	45.4	0.06
21	F	3.28	98.0	195.0	29.6	0.22
22	F	0.95	102.0	157.0	57.9	0.06
23	F	0.90	104.0	124.0	22.1	0.06
24	M	0.99	106.0	156.0	50.4	0.07
25	M	1.00	106.0	160.0	54.2	0.07
26	M	1.37	108.0	147.0	28.4	0.09
27	F	0.97	109.0	160.0	52.6	0.06
28	F	1.07	110.0	173.5	59.6	0.07
29	M	0.94	111.0	156.0	47.9	0.06
30	F	1.56	114.0	155.0	26.2	0.10
31	F	2.20	117.0	184.0	30.5	0.14
32	F	1.69	117.5	175.5	34.3	0.11
33	M	0.90	118.0	152.0	37.7	0.06
34	M	1.48	120.0	167.0	31.8	0.10
35	M	0.91	121.0	161.0	43.9	0.06
36	F	1.37	124.0	173.0	35.7	0.09
37	M	0.91	124.0	137.0	14.2	0.06
38	F	0.93	149.0	164.0	16.2	0.06
39	M	1.16	170.0	193.6	20.3	0.08
40	F	5.28	190.0	235.0	8.5	0.35
41	F	1.20	281.0	288.0	5.8	0.08
42	M	3.33	287.0	317.5	9.2	0.22
218097	F	0.94	104.0	141.0	39.4	
304303	M	0.98	70.5	112.0	42.3	
190804	F	1.19	100.0	158.0	48.7	
204379	M	1.06	93.5	145.0	48.4	

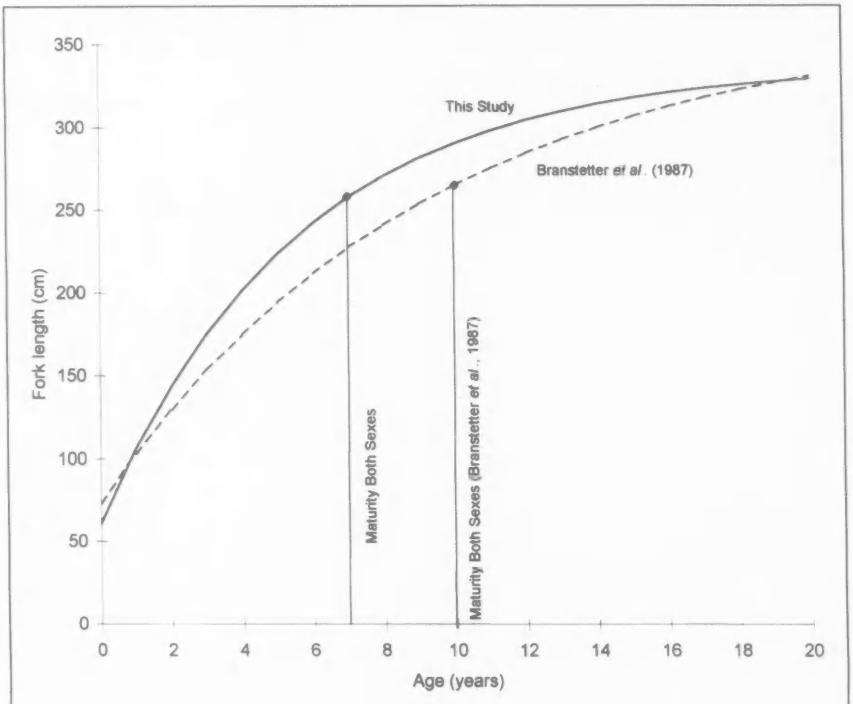

Figure 2

Tag-recapture growth curve derived in this study by using the Gulland and Holt (1959) method compared with the growth curve derived by Branstetter et al.'s (1987) using Atlantic Ocean vertebral data. Estimated size and age at maturity are included on both curves.

Table 2

VBGF parameters calculated by using two different tag-recapture methods (Gulland and Holt, 1959, and Fabens, 1965) (n=42) and compared with Branstetter et al.'s (1987) estimates derived from vertebral analysis (fork lengths calculated by using Branstetter et al.'s (1987) conversions).

Model	L_∞	SE	k	SE	t_0
Gulland and Holt, 1959	337 FL	6.95	0.178	0.048	−1.12
Fabens, 1965	293 FL	19.10	0.217	0.031	−1.08
Branstetter et al., 1987					
Atlantic	440 TL (365 FL)	0.107	−2.35		
Gulf of Mexico	388 TL (324 FL)	0.184	−1.13		

therefore, appears to be more appropriate for sharks (Cailliet et al., 1992).

In this study, the Gulland and Holt (1959) method produced more biologically reasonable results than the Fabens (1965) method. The L_∞ calculated from the Gulland and Holt method was 337 cm FL, which is lower than the maximum reported western North Atlantic values from the literature (391 cm FL; Bigelow and Schroeder, 1948). More recently, in the western North Atlantic and Gulf of Mexico, the largest sharks observed were 346 cm FL (Branstetter, 1981) and 339 cm FL[3] the latter quite close to our

[3] Kohler, N. E., H. W. Pratt Jr., L. J. Natanson, P. Turner, and R. Briggs. 1996. The shark tagger 1995 summary. Narragansett Laboratory, Northeast Fish. Science Center, Natl. Mar. Fish. Serv., NOAA, 16 p.

estimate. However, the tiger shark has been reported to 469 cm FL (Castro, 1983). The L_∞ value estimated from the Fabens (1956) method (293 cm FL), however, is lower than all reported values. In addition, the Fabens (1965) method value for k is high (Table 2). We therefore concluded that the Gulland and Holt (1959) VBGF is the more appropriate model to use for the tiger shark. Cailliet et al. (1992) and Van Dykhuizen and Mollet (1992) also preferred the Gulland and Holt (1959) model over that of Fabens (1965) for the angel and sevengill sharks, respectively.

Data from this study indicated that neither tagging nor tagging combined with OTC injection appears to retard the growth rate in neonate and juvenile sharks up to 150 cm FL (Fig. 3). To the contrary, the growth rates from tagged sharks were higher than estimates obtained from vertebral growth bands (Table 3). The growth rates for the first two years of life for the tiger shark estimated from monthly length frequencies, tag-recapture (Gulland and Holt, 1959), and tag-recapture with OTC were all similar (Fig. 3). Tanaka (1990) found that growth rates of OTC-injected Japanese wobbegongs, *Orectolobus japonicus*, and neonate swell sharks, *Cephaloscyllium umbratile*, were not significantly different from controls. More recently, Gelsleichter et al. (1998) evaluated the toxicity of OTC on growth rates of captive nurse sharks, *Ginglymostoma cirratum*, and concluded that there were no adverse effects of OTC on growth rate. These data support the use of OTC as an effective method for determining vertebral band periodicity without interrupting normal growth patterns (Tanaka, 1990; Gelsleichter et al., 1998).

Our data do not verify nor refute age estimates for the tiger shark previously obtained from vertebral band counts (Branstetter et al., 1987) (Table 2; Fig. 2). The k value from our study is higher than Branstetter et al.'s (1987) Atlantic value and our L_∞ is lower. These differences are to be expected when comparing VBGF parameters from a conventional age-length (vertebral methods) study with those derived from a growth increment (tagging) study (Sainsbury, 1980; Francis, 1988). These types of curves are not directly comparable because the parameters are derived differently and, therefore, have different meanings (Francis, 1988). However, comparison of the estimates obtained in these studies to known values, such as size at birth and maximum size, can provide insight into the fit of the curves. This information allows us to determine which curve is best suited to be used for age at maturity and maximum age estimates. We believe that the current tag-recapture values are more accurate on the basis of verification available from the monthly length-frequency analysis and the consistency of the estimates to measurable parameters such as size at birth and maximum size. The L_∞ calculated by Branstetter et al. (1987) is lower than maximum reported sizes, and the size at birth (73 cm FL), based on the von Bertalanffy curve from that study, was high as related to known parameters (60–65 cm FL[1]).

Table 3

Size at age and growth per year for the tiger shark, *Galeocerdo cuvier*, calculated for tag and recapture data with Gulland and Holt's (1959) (this study) method compared with Branstetter et al.'s (1987) Atlantic vertebral data. Approximate size at maturity is indicated by bold typeface.

	Size (cm, FL)		
Age (years)	This study	Branstetter[1] 1987	This study growth/yr (cm)
Birth	61	73	
1	106	103	45
2	144	130	38
3	175	153	32
4	202	175	26
5	224	194	22
6	242	212	18
7	**258**	227	15
8	271	241	13
9	281	254	11
10	290	**265**	9
11	298	275	8
12	304	284	6
13	310	293	5
14	314	300	4
15	318	307	4
16	321	313	3
17	324	318	3
18	326	323	2
19	328	327	2
20	329	331	2

[1] Branstetter et al. (1987) values converted to FL.

Statistically significant differences between age estimates from the Gulf of Mexico and North Atlantic populations of tiger shark found by Branstetter et al. (1987) may not be biologically significant (Yoccoz, 1991). The differences in age at maturity obtained between these two areas is only 2–3 years. Considering the relatively slow growth and large overlap of size at age for this species, a 2–3 year difference could be included in the realm of measurement error. In addition, we found statistically significant differences in growth by year in first year tiger sharks obtained from the same region over a period of five years. The differences in growth between years indicate that tiger shark growth is quite variable and probably dependent on fluctuations of many parameters in-

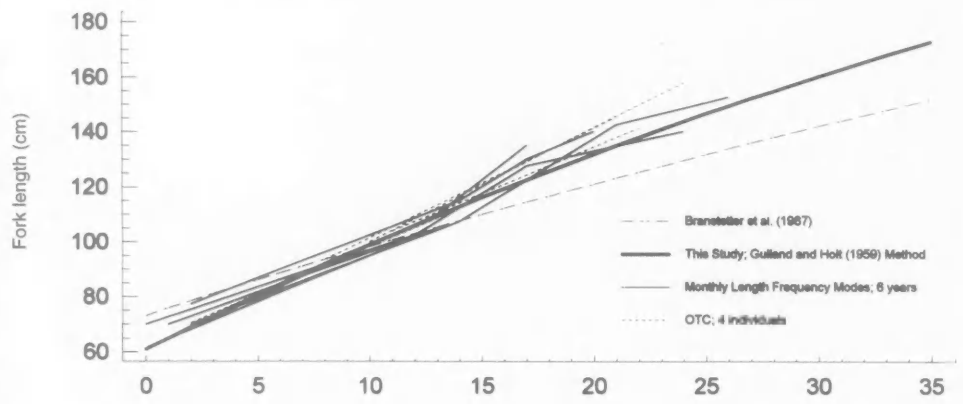

Figure 3

The von Bertalanffy growth curves from tag-recapture analysis was estimated with the Gulland and Holt (1959) model and the von Bertalanffy growth curve estimated from vertebral analysis (Branstetter et al. 1987). The solid lines represent the individual monthly length-frequency mode data from six year classes (1988–93). The initial points of the line are set by the size in June of the birth year. The solid lines are actual growth of four individual OTC-injected recaptured sharks at liberty over 0.9 yr. The length at tagging was used to obtain the initial age estimate to set the point on the graph.

cluding environmental conditions and prey availability. Our data show that that the majority of neonatal tiger sharks remain in the nursery area from birth until about 120–150 cm FL or 1.5–2 years of age.[1] It is known that tiger sharks frequently migrate into and out of the Gulf of Mexico (Kohler et al., in press). It is doubtful, with the migratory nature of this species and mixing between these areas, that growth rate differences in these groups are biologically significant past perhaps the first three years of life.

The longevity of the tiger shark is difficult to estimate. The NMFS tagging program has received data on five tiger sharks at liberty for 6 to 11 years. The oldest of these fish would have been 3+ years at tagging (185 cm FL, estimated), on the basis of the Gulland and Holt (1959) growth curve and, therefore, 14+ years at recapture (325 cm FL, measured). Branstetter et al.'s (1987) oldest aged tiger shark was 16 years of age. Our longevity estimate, based on a 7 half-life criterion, indicated that tiger sharks may live to be at least 27 years of age. Branstetter et al. (1987) estimated maximum age at anywhere from 20–37 years based on L_∞ for their various VBGF curves and rate of growth of large individuals.

Based on revised growth estimates presented in this study, estimated maximum age for this species is 27 years. Age at maturity, estimated from tag-recapture data from this study and size at maturity estimates from Branstetter et al. (1987), is seven years suggesting that females mature at 25% of their maximum age and may reproduce 10 times based on a two-year reproductive cycle.

Overall, the tiger shark is similar to other large carcharhinids in that it grows slowly and has a relatively long life, although it matures earlier than many other species in the northwest Atlantic (*C. leucas* 14–18 years, Branstetter and Stiles, 1987; *C. plumbeus* 15–30 years; Casey and Natanson, 1992, Sminkey and Musick, 1995; *C. obscurus* 19–20 years; Natanson, 1994; *C. falciformis* 6.5–12 years, Branstetter, 1987c, Bonfil et al., 1993). Branstetter (1987b) discussed the various life strategies of sharks on the basis of their k values. He suggested that tiger sharks, with k values from 0.11 to 0.16, fit into an intermediate category between slow growth species (k=0.05-0.10) such as *C. plumbeus, C. obscurus, Negaprion brevirostris,* and *Sphyrna lewini* and fast growth species ($k \geq 0.2$) such as *C. limbatus, C. brevipinna, Rhizoprionodon terraenovae*, and *Prionace glauca.* Other sharks in the intermediate group include *C. acronotus and C. falciformis* according to Branstetter (1987b). The tiger shark reaches maturity at a lower percent (25%) of its total age than do other carcharhinids for which this parameter has been estimated (*S. lewini* 33–50%, Branstetter, 1987c). This finding suggests that the tiger shark has a longer reproductive life span and possibly a greater reproductive potential than other carcharhinids.

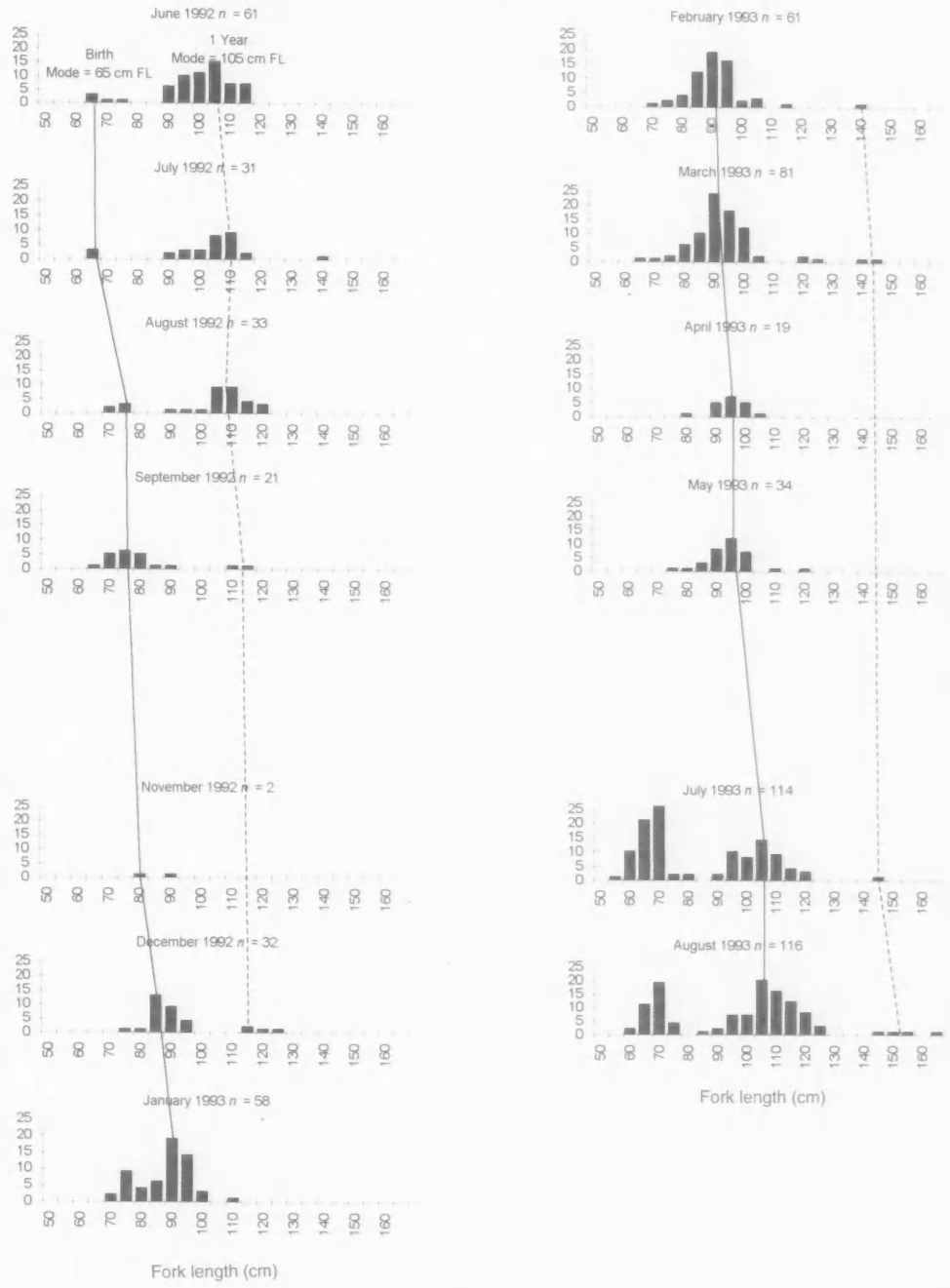

Figure 4

Monthly length-frequency data for the 1992 year class used for obtaining length-frequency growth rates for small (<160 cm FL) tiger sharks in the nursery area. First and partial second year growth for the 1992 year class is represented with the solid line. Second and partial third year growth for the 1991 year class is represented by the dashed line.

Casey and Natanson (1992) showed the advantage of using tag-recapture data over vertebral analysis for aging the sandbar shark. Cailliet et al. (1986) reviewed the techniques available for determining age and verifying age estimates in elasmobranchs. They pointed out that ages estimated from growth zones in calcified hard parts need to be verified with other methods, such as length-frequency and tag-recapture analyses. The authors also stressed the importance of validating the temporal periodicity of the calcified bands with tag-recapture data from the laboratory or field, coupled with OTC marking. Cailliet (1990), in an update of the Cailliet et al. (1986) review, listed the studies, to that date that had employed the various verification methods. Several of these used the combination of tag-recapture, length-frequency and OTC marking for verification or validation (or both) of the calcified structure age estimates. Growth estimates from a laboratory and field study of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) (Branstetter 1987a) corresponded well to estimates generated with length frequencies and vertebral rings (Parsons, 1985). Casey et al. (1985) used length-frequency, vertebral and tag-recapture analyses to verify age estimates for the sandbar shark, *C. plumbeus*, and concluded that there was close agreement with all three methods. Pratt and Casey (1983) also used these three methods to age the shortfin mako, *Isurus oxyrinchus*, and concluded that not only was there agreement between the methods but that tagging did not affect growth in this species. Smith (1984) validated the periodicity of vertebral band deposition in the leopard shark, *Triakis semifasciata* using OTC. Kusher et al. (1992) were able to confirm these results as well as use length-frequency data and additional tag-recapture data to produce independent age estimates for this species. The tag-recapture curve gave slower k values than the vertebral, and although the k values were not significantly different, the authors suggested that tagging may have had an effect on growth in this species (Kusher et al. 1992). These results accentuate the requirement of good tag and recapture data as a backup for vertebral studies, particularly if combined with OTC injections for validation. In the case of the tiger shark in this study, tag-recapture and length-frequency data have provided independent estimates of growth for verification. In addition, the results present evidence against the suggestion that tagging, with or without OTC injection, decreases the growth rate of sharks. It can be argued that the tiger shark cannot be used to generalize about sharks because they grow rapidly in relation to many other species. A birth size of 61 cm FL with a corresponding weight of 1.8 kgs. is small in relation to many large coastal species, such as the dusky shark (size and weight at birth: 81 cm FL and 7 kgs., respectively, Castro, 1983; Kohler et al., 1995) and the silky shark (size and weight at birth: 64 cm FL and 9 kgs., respectively). If these relatively small tiger shark young can withstand the rigors of tagging and continue to grow at a similar rate as untagged individuals, then it is certainly reasonable to believe that a larger shark can as well. Regardless, all species need to be evaluated individually for their reactions to tagging and OTC injection.

Acknowledgments

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Recruitment of Atlantic croaker, *Micropogonias undulatus*: Do postsettlement processes disrupt or reinforce initial patterns of settlement?*

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Abstract.—Understanding the relative importance of pre- and postsettlement processes is critical to understanding the population dynamics of marine fishes. Our goals in this study were 1) to examine habitat preference and habitat use of newly settled Atlantic croaker, *Micropogonias undulatus*, and 2) to determine if postsettlement growth or predation varied with habitat type. Field surveys showed no difference in croaker abundance among three estuarine habitats: marsh edge, seagrass, and sand. Behavioral experiments in laboratory mesocosms suggested that the pattern of similar use of habitats in the field results from a lack of preference among habitats. In a field experiment, croaker recruitment was greater to artificial seagrass than to sand habitats, but there was no difference in fish density in habitats with or without food supplementation. Moreover, growth rates were similar in both sand and artificial seagrass habitats and in habitats with or without food supplementation. In a second experiment, we were unable to detect a difference in the density of newly settled croaker between sand and artificial seagrass habitats, or between habitats with predator access limited by cages and cage controls. Our results demonstrate that newly settled croaker use different estuarine habitats similarly, and there does not appear to be a fitness consequence of using many habitats. We suggest that for habitat generalists, such as the Atlantic croaker, variability in larval supply will be a stronger predictor of population dynamics than will variability of habitat attributes.

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Understanding the causes of fluctuations in population abundance is critical for ecologists and fishery biologists. For marine fishes with life histories in which adults have limited home ranges and larvae are pelagic and advected vast distances from natal sites, an understanding of variability in larval supply to local populations is critical for understanding the mechanisms that produce dynamics in populations (Caley et al., 1996). In addition, habitat selection by settling fish (Carr, 1991; Levin, 1991; Wellington, 1992; Tolimieri, 1995), and habitat-specific growth and mortality (Heck and Orth, 1980; Hixon and Beets, 1993; Levin et al., 1997) may ultimately reinforce or disrupt patterns created by variable larval supply (Jones, 1997). Thus, knowledge of the degree to which processes such as habitat selection, competition, or predation modify initial patterns of larval settlement is important in understanding the population dynamics of marine species.

The importance of variability in postsettlement growth or mortality and the level to which postsettlement processes alter initial patterns of larval settlement can be a function of habitat structure. For example, on coral reefs, holes provide a refuge from predation, and on reefs with large numbers of holes, the importance of predation is reduced (Shulman, 1984; Hixon and Beets, 1993). Similarly, Atlantic cod settle in equivalent densities in a variety of habitats but suffer lower predation rates in structurally complex habitats (Tupper and Boutilier, 1995). Thus, habitat-specific mortality disrupts initial patterns of larval settlement. Differences in habitat structure may also impact growth rates or the ability of fish to procure food (Nelson, 1979; Heck and Thoman, 1981; Stoner, 1982). As examples, 1) pinfish have greater success capturing amphipods in shoal grass (*Halodule wrightii*) than in similar densities of turtle grass (*Thalassia testudinum*) (Stoner,

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1982); 2) Atlantic cod grow faster in seagrass habitats than in sand, rocky reef, or cobble habitats (Tupper and Boutilier, 1995); and 3) pinfish exhibit higher growth rates in seagrass than in sand habitats (Levin et al., 1997).

Atlantic croaker, *Micropogonias undulatus* (hereafter referred to as croaker), range from Cape Cod to Campeche Bank, Mexico (Johnson, 1978), and occur both offshore and in estuaries in a variety of habitats including mud, sand, and seagrass (White and Chittenden, 1977; Johnson, 1978; Rooker et al., 1998). Croaker are an important component of commercial fisheries in the Gulf of Mexico and southeastern United States, often dominating bottom fish landings, and are an important sport fishery in this region (Lassuy, 1983). In the Gulf of Mexico, croaker spawn over the continental shelf or near inlets from September to May with peak levels occurring before January (Johnson, 1978; Cowan, 1988; Cowan and Shaw, 1988). Larval croaker then move toward shore and may be transported hundreds of kilometers before entering estuarine nursery grounds (Cowan and Shaw, 1988; Norcross, 1991). In Texas, recruitment of croaker peaks in November (Rooker et al., 1998). It is not clear whether variability in abundance of juvenile croaker is the result of variability in larval supply or differential postsettlement growth and mortality.

The delivery of larval croaker recruits to estuarine nursery habitats is dependent on large-scale oceanographic processes (Cowan and Shaw, 1988). Once fish arrive at estuaries, delivery into suitable habitats is dependent on currents and tidal processes (Norcross, 1991). As fish that are competent to settle approach nursery grounds they have the opportunity to choose specific microhabitats. In this paper we examined patterns of microhabitat preference and use by newly settled croaker, as well as the consequences of microhabitat associations. Specifically we asked 1) Do croaker have specific microhabitat preferences and are these preferences reflected in patterns of abundance in the field? 2) Does food supply limit the number or growth rates of croaker recruits in different habitats? 3) Does predation determine the number of recruits in different habitats?

Methods

Habitat use by newly recruited croaker

To determine what habitats newly recruited Atlantic croaker use, we conducted a field survey during November 1996 at Christmas Bay (29°03'N, 95°10'W), near Galveston, TX. Christmas Bay is a shallow estuary and contains the most easterly well-developed seagrass bed in Texas. A detailed description of this site can be found in Thomas et al. (1990). The seagrass bed is dominated by *Halodule wrightii* with an average density of 10,469 shoots/m^2 (SE=461). An epibenthic sled was used to quantify fish abundance in three habitats: bare sand, seagrass meadow, and marsh edge. We defined marsh edge habitat as the subtidal substrata directly adjacent to a *Spartina alterniflora* marsh. The sled consisted of a 0.66 m × 0.5 m opening fitted with a 3-m long net (1-mm mesh) with a removable codend. Habitats were sampled by placing the sled on the substratum, extending a 15-m rope in a semicircular fashion (to avoid disturbing sampling area) and pulling the sled through a 10-m^2 area. Each habitat was sampled four times at two different sites, resulting in eight samples per habitat type. Differences in croaker density were examined with a two-way analysis of variance with both site and habitat type as fixed effects. In this and subsequent analyses, if we failed to reject the null hypothesis of no difference in croaker abundance between habitats, then power analysis was performed. If statistical power was low, we calculated the number of replicates required to achieve sufficient power to accept the null hypothesis.

To examine habitat preference we performed choice experiments in laboratory mesocosms. Six 117-L mesocosms were constructed from round circular plastic tanks (41.3 cm diameter × 60 cm). The mesocosms were filled with 5 cm of sand, a plastic mesh screen was placed on top of the sand, and an additional 5 cm of sand was placed over the mesh. Each tank was filled with filtered seawater and maintained at ambient light and temperatures. We divided mesocosms in half, with each half randomly receiving a sand or grass habitat. Sand habitat was the sand bottom described above. To construct seagrass habitats, cores of seagrass were randomly collected from the field and brought to the laboratory where they were washed and dipped in fresh water. After leaves were wiped to remove any epiphytic growth, the cores were planted in each mesocosm.

One croaker (15–20 mm SL) was introduced to the center of each mesocosm and monitored for any abnormal behavior for 24 h. After the initial acclimation period, the location of each croaker was visually determined hourly for ten consecutive hours. Visual observations were performed by a single observer peering into the mesocosm, without disturbing the fish. This was repeated for six mesocosms over two days for a total of 12 mesocosm observations. New fish were used for each trial. Percent occurrence in each habitat was determined for all twelve trials. A one-way *t*-test determined if percent occurrence in seagrass was different from 50%.

Effects of food supply on recruitment and growth of croaker in varying habitats

Field experiments were conducted in East Lagoon, located at the eastern most end of Galveston Island, TX (29°20'N, 94°44'W). East Lagoon is 1.6 km long, 0.48 km wide, and has a maximum depth of 4.6 m. Water is exchanged tidally by means of seven 0.92 m-diameter cement culverts with the Galveston Ship Channel, which runs from the Gulf of Mexico into Galveston Bay. A detailed description of this site can be found in Levin et al. (1997). Seagrass, once widespread in Galveston Bay, including East Lagoon, has decreased by 90% from peak levels (Pulich and White, 1991); no natural seagrass habitats presently are found in East Lagoon. The absence of natural seagrass beds allowed us to establish artificial seagrass beds with desired characteristics, without the confounding effects of a natural seagrass bed. Experiments were located >8 m from the *Spartina alterniflora* dominated marsh edge and placed at an average low tide depth of 42 cm.

To test the null hypothesis that food supply does not limit abundance or growth rates of croaker recruits in different habitats, we conducted an experiment in which food supply was manipulated in sand and seagrass habitats. On 20 February 1996 we created five blocks each consisting of four 1-m^2 experimental plots. Within each block, food supply and habitat type were manipulated orthogonally. To control for differences in seagrass structure or seagrass-associated food resources, we used artificial seagrass habitats. Artificial seagrass habitats were constructed from a 1-m^2 polyvinylchoride (PVC) (1.3 cm diameter) frame, strung with monofilament to form a grid consisting of 576 points. At each of these points a 16 cm × .5 cm strand of green ribbon was woven in, such that the frame consisted of 576 shoots of seagrass, each shoot having two leaves. No excessive fouling was observed on the frame or ribbon for the duration of the experiment. We performed a preliminary experiment to determine if the structure of the PVC-frame would attract more fish recruits than bare sand, and no difference was found between the bare sand plot and the PVC-frame ($F_{2,23}$=0.512, α=0.61, 1–β=0.76). Consequently we performed subsequent experiments without a PVC-frame control.

Food supply was experimentally manipulated with feeding tubes in each experimental plot. Feeding tubes were constructed of a 7.5-cm diameter length of PVC pipe attached to a 1.3-cm diameter PVC pipe stake, with the bottom of the tube about 15 cm from the substratum, and the top always above the water line. We provided supplemental food daily for seven days, from 23 February to 3 March 1996, to half of the sand and seagrass replicates (i.e. five sand and five seagrass plots received food). Food consisted of 200 g of fish flesh and 300 mL of water blended to produce plankton-size particles (Forrester, 1990; Levin et al., 1997). The fish purée was placed in ice cube trays and frozen. Each frozen cube yielded 11.8 g of fish flesh. One cube of frozen food was placed in the feeding tubes of appropriate replicates, whereas control plots received one ice cube and no food was added. As the ice cube containing food melted, it delivered a continuous stream of particles to the habitat for 5–15 min. We observed fish readily consuming the supplemented food in both the field and laboratory.

On 4 March 1996, the experiment was terminated by sampling each plot. Recruit density was quantified by using 1 m^3 (1 × 1 × 1 m) drop samplers (Zimmerman et al., 1984; Fonseca et al., 1990). Drop samplers were constructed of 9.5-mm diameter rebar covered on four sides with taut 2-mm nylon mesh. A dip net (90 × 100 cm, 2-mm nylon mesh) was used to retrieve fish from the samplers, and replicates were considered adequately sampled when five consecutive passes of the dip net yielded no fish (Fonseca et al., 1990). A blocked two-factor analysis of variance was used to test the hypotheses that the abundance of newly recruited croaker did not vary among habitat or food supplemented treatments.

Five fish from each replicate were haphazardly selected for further analysis. We measured the 80 selected fish to the nearest 0.1 mm (SL), removed their otoliths, and stored them in immersion oil for one week. Fish age was then determined by enumerating the daily growth rings on the lapillar otolith by using an image analysis system. The existence of daily rings on croaker otoliths has been validated previously (Nixon and Jones, 1997). Each otolith was examined independently three times. If two of the three counts did not agree, the fish was discarded and another selected. When two of the three counts were the same, that count was used as a datum in the analysis.

Differences in growth rates were examined by using otolith microstructure. Because otolith diameter was correlated to fish length (r=0.73, n=75), we used otolith measures as a proxy for growth rate. Measurements were taken inward from the edge of the otolith to the seventh ring. This distance corresponded to growth during our seven days of food supplementation. Otolith distances (μ) were then converted into daily growth rates (mm SL/day), by using the following equation generated from a regression of otolith diameter on fish length:

$$Growth = [(otolith\ distance + 0.002) / 0.014]/7.$$

We used a blocked two-factor analysis of variance to test the hypothesis that growth rates did not vary among habitat or food supplementation treatments.

Effects of predation on recruitment of croaker to varying habitats

The null hypothesis that predation has no effect on recruitment of croaker in sand or seagrass habitats was tested by using cages to limit predator access to experimental plots. On 18 March 1996, a fortuitous seasonal low tide completely exposed the study site to air, allowing us to erect cages and to ensure that no recruits or predators occupied the cages at the start of the experiment. Cages ($2 \times 2 \times 1$ m) were constructed with 25-mm mesh on four sides, whereas cage controls had mesh on two sides. Mesh was large enough to be transparent to croaker recruits, but fine enough to prevent predators from entering the cages. A randomized block design was employed, with habitat (sand or grass) and predator access (cage or cage control) as fixed effects. Replicates were placed 8 m apart, and blocks were separated by 10 m. The experiment was terminated after 7 d. Drop samplers were used to quantify recruits as described previously.

Results

Habitat preference and use by newly recruited croaker

The density of newly settled croaker (mean TL=14.48, SE=0.15) did not differ among sand, seagrass, or marsh edge habitats ($F_{2,18}$=0.86, α=0.44, β=0.13) (Fig. 1). The density of croaker recruits also did not vary between sites ($F_{1,18}$=0.09, α=0.77) and the interaction between habitat and site was not significant ($F_{2,12}$=1.07, α=0.37).

Our observation on the behavior of croaker recruits in mesocosms did not reveal a preference between sand and seagrass habitats (one way t-test, t=1.64, df=11, α=0.13). An average of 36% (SE=16) of the time was spent in seagrass, and 64% (SE=16) in sand.

Effects of food supply on croaker recruitment and growth in varying habitats

The abundance of newly settled croaker differed between experimental habitats ($F_{1,11}$=5.98, α=0.03) with greater recruitment in sand ($\overline{X}$=31.6/m^2, SE=6.5) than in seagrass habitats ($\overline{X}$=13.7/m^2, SE=5.9) (Fig. 2). Conversely, we did not detect a difference ($F_{1,11}$=0.13, α=0.73) in the number of croaker in food-supplemented plots ($\overline{X}$=23.2/ m^2, SE=8.3), compared with control plots ($\overline{X}$=22.1/m^2, SE=4.1) (Fig. 2). The interaction between habitat and food-supplementation was not significant ($F_{1,11}$=0.96, α=0.35). The statistical power of this experiment was low (1–β=0.18);

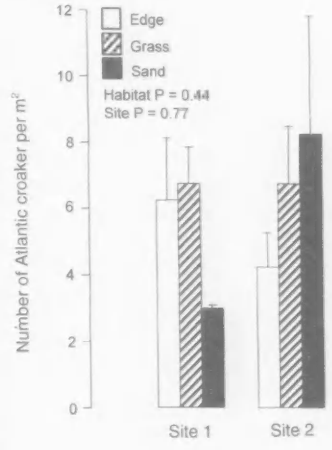

Figure 1

Atlantic croaker densities (mean +1 SE) sampled from three estuarine habitats: marsh edge (edge), seagrass bed (grass), and barren sand (sand). P values from two-way analysis of variance.

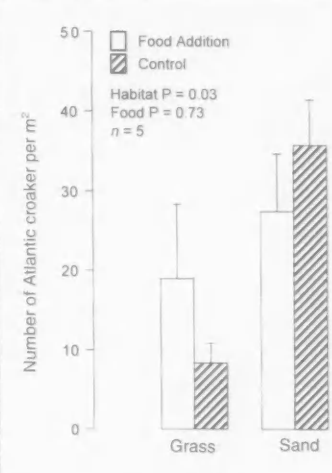

Figure 2

Atlantic croaker density (mean +1 SE) in 1-m^2 artificial seagrass (grass) and sand habitats, with (food addition) and without (control) food supplementation. P values from a blocked two-factor analysis of variance.

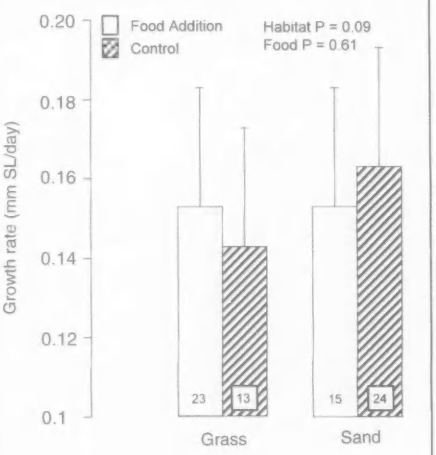

Figure 3

Growth rate (mean +1 SE) determined from analysis of otolith microstructure in croaker from 1-m^2 artificial seagrass (grass) and sand habitats with (food addition) and without (control) food supplementation. *P* values are from a blocked two-factor analysis of variance, and *n*, the number of fish sampled, is given at the base of each bar.

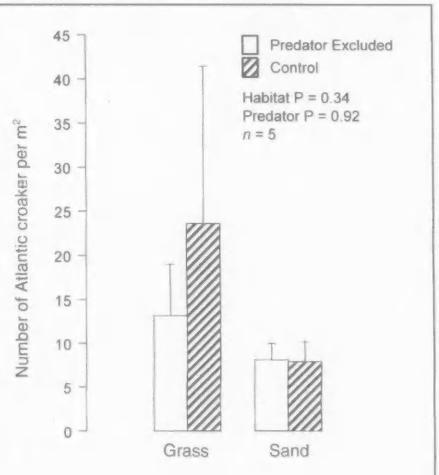

Figure 4

Atlantic croaker density (mean +1 SE) in 1 m^2 artificial seagrass (grass) and sand habitats with predators excluded and allowing predatory fish and decapod access (control). *P* values from a blocked two-factor analysis of variance.

however, given the small difference in average croaker density between food-supplementation and control plots (1.1/m^2) and the high within-treatment variation, we would have needed 55 replicates to achieve sufficient power ($1-\beta=0.95$) to accept the null hypothesis of no difference between treatment means.

Growth rates of newly recruited croaker were the same in sand and grass habitats ($F_{1,70}=2.79$, $\alpha=0.09$, $\beta<0.001$), as well as with or without food supplementation ($F_{1,70}=0.26$, $\alpha=0.61$, $\beta=0.004$) (Fig. 3). The interaction between habitat and food-supplementation on the growth rate of newly recruited croaker was not significant ($F_{1,70}=0.49$, $\alpha=0.49$). Growth averaged 0.148 mm SL/day (SE=0.03) in grass and 0.158 mm (SE=0.03) in sand. Average growth rates of 0.153 mm/day (SE=0.03) were observed for both control and food addition treatments (Fig. 3). These growth rates are similar to growth rates reported elsewhere (Warlen, 1981; Cowan, 1988; Nixon and Jones, 1997), suggesting that our back calculation of growth rates from otolith measures were not seriously biased.

Effects of predation on recruitment of croaker to varying habitats

When we examined recruitment of croaker to experimental plots with or without predator access, we were unable to detect an effect of predation on croaker recruitment ($F_{1,12}=0.01$, $\alpha=0.92$) (Fig. 4). Croaker density averaged 10.7/m^2 (SE=3.8) in the caged replicates, and 15.8/m^2 (SE=10.1) in cage controls (Fig. 4). In contrast with the food supplementation experiment, we did not detect a difference in recruitment between grass and sand habitats ($F_{1,12}=0.96$, $\alpha=0.34$) (Fig. 4). The interaction between habitat and predator access was also not significant ($F_{1,12}=0.10$, $\alpha=0.76$). This experiment also suffered from low power ($1-\beta=0.06$). Sufficient power to accept the null hypothesis of no difference in croaker density between cage and cage-control treatments ($1-\beta=0.95$), would have required 550 replicates.

Discussion

Recruitment of fishes with open populations is affected by variability in larval supply (Jenkins et al., 1996; Hamer and Jenkins, 1997), habitat selection by settling larvae (Bell et al., 1987) and postsettlement mortality (Orth et al., 1984), growth (Levin et al., 1997), and migration (Sogard, 1989). Understanding how these processes interact with each other to determine population size has been a major focus of researchers on tropical and temperate reefs (Doherty and Williams, 1988; Caley et al., 1996) and recently in seagrass meadows (Bell et al., 1987; Jenkins et al., 1996; Hamer and Jenkins, 1997). There has also

been a growing awareness that understanding how demographic processes vary with habitat structure will be critical for predicting population size in fishes that occur in heterogeneous habitats (Levin, 1994). In this study we examined patterns of abundance of newly settled Atlantic croaker and demonstrated that these fish use different estuarine habitats similarly. The results of our mesocosm experiment suggest that the pattern of similar recruitment in different habitats results from a lack of preference for specific habitats. In addition, when we investigated habitat differences in postsettlement growth or survivorship, we were unable to detect strong consequences of using one habitat over another.

We found no evidence suggesting that habitat selection by settling larvae and habitat-specific postsettlement mortality are important in determining population size in croaker; however, this conclusion is based on nonsignificant statistical tests rather than explicit acceptance of the null hypothesis of no difference between treatments. Recent reviews have stressed the importance of power analysis in detecting a type-II errors (Peterman, 1990; Reed and Blaustein, 1995; Thomas and Juanes, 1996), and because we wished to draw conclusions from "negative" results, power analysis was particularly important. In this study, when a difference between treatment means was not detected, we examined power in an attempt to determine our ability to accept the null hypothesis. If the power of the test was too low to accept the null hypothesis ($\beta \leq 0.05$), the number of replicates required to achieve this power level was calculated. For example, no difference was detected in mean croaker number between plots from which predators were excluded and control plots, but the power of this experiment was low ($1-\beta=0.06$). Sufficient power to be able to accept the null hypothesis, would have required 550 replicates. Our level of replication was inadequate because of the extreme variability in croaker densities among experimental plots—variation likely produced by a combination of stochastic settlement and habitat-specific mortality. The effect of this variability was to weaken the power of our experiments to detect small, but real differences among treatments. Although our experimental design precluded the detection of small treatment effects, the high number of replicates required to detect these small effects suggests that other processes are likely to be more important in determining variability in abundance.

Although many estuarine species select vegetated over unvegetated habitat at settlement (Orth et al., 1984), in some cases, initial patterns of settlement have little to do with habitat selection by individual organisms. Settlement may occur at the first suitable habitat encountered regardless of specific attributes of that habitat (Bell and Westoby, 1986). Additionally, current patterns may exclude delivery of competent larvae to some habitats (Morgan et al., 1996); therefore, even ideal habitats may seldom receive recruits. In such cases, larvae do not select against a habitat, instead that habitat is never an available choice. By experimentally providing habitats, and by using a blocked sampling design such that all habitats were available in a particular location, we eliminated the possibility that settling croaker would not have the opportunity to choose a habitat. In our field sampling and experiments, croaker had the opportunity to choose between vegetated and unvegetated habitats, but they did not consistently choose one habitat over another. By contrast, in an identical experiment performed at the same time and in the same study site, pinfish (*Lagodon rhomboides*) showed strong responses to habitat, food supply, and predators (Levin et al., 1997). Pinfish occurred in much higher densities in vegetated than in unvegetated habitats and also grew faster in grass habitats supplemented with food than in unsupplemented or unvegetated habitats. In addition, the presence of predators reduced pinfish numbers by 50%. The pinfish and croaker occupying experimental plots were similar in size (15–25 mm SL), and at this size the diets of the two species are similar (Darcy, 1985; Soto et al., 1998). Thus, it is likely that the lack of response by croaker to the habitat attributes we investigated is the result of characteristics of the species rather than an artifact of sampling or experimental design.

Selection for specific habitats at settlement may overwhelm variation in larval supply, thus producing variability in recruitment that is associated with the preferred habitat. This appears to be the case for pinfish (Levin et al., 1997). Although croaker often form part of fish assemblages within seagrass (Rooker et al., 1998), they appear to have broad microhabitat preferences, and our results suggest that there is no strong fitness consequences for croaker using vegetated versus unvegetated habitats. As a result, resources associated with the benthic habitat seem unlikely to determine population size of newly recruiting croaker. Rather, where and when larvae that are competent to settle are delivered should determine population size in croaker. The contrasting results for croaker and pinfish may reflect a more general difference in the processes determining population sizes of fish. For fishes, such as pinfish, where settling larvae select specific habitats and postsettlement processes reinforce initial settlement patterns, spatial and temporal variability in habitat should be a strong predictor of future

population size. Habitat generalists, such as croaker, can occupy a range of habitats in any particular location, and thus variability in a specific resource may not determine population size. Consequently, processes affecting larval supply will be more important predictors of population size than resource-related characteristics.

Generalizations about the relative importance of processes affecting recruitment in fishes have been elusive (Caley et al., 1996). Although it is widely recognized that understanding the roles of both pre- and postsettlement is critical, there is still little consensus on the relative importance of different processes in determining population size. We suggest that neglecting the behavioral and ecological characteristics of individual species may be a major obstacle in reaching widely accepted generalizations about processes affecting recruitment. By performing similar experiments on different species we may uncover generalizations about processes affecting fish populations that have thus far been difficult to attain.

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Temporal and geographic variation in fish communities of lower Cook Inlet, Alaska

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Abstract.—Nearshore and shelf fish communities were studied in three areas of lower Cook Inlet, Alaska: the Barren Islands (oceanic and well-mixed waters), Kachemak Bay (mixed oceanic waters with significant freshwater runoff), and Chisik Island (estuarine waters). Fish were sampled with beach seines (n=413 sets) and midwater trawls (n=39 sets). We found that lower Cook Inlet supported a diverse nearshore fish community of at least 52 species. Fifty of these species were caught in Kachemak Bay, 24 at Chisik Island, and 12 at the Barren Islands. Pacific sand lance dominated Barren Islands and Kachemak Bay nearshore habitats, comprising 99% and 71% of total individuals, respectively. The nearshore Chisik Island fish community was not dominated by any one species; instead it exhibited higher diversity. These spatial differences appeared linked to local oceanographic regimes and sediment influx. Analysis of historical data revealed that the nearshore Kachemak Bay fish community changed significantly between 1976 and 1996, showing increased diversity and abundance in several taxa, notably gadids, salmonids, pleuronectids, and sculpins. Decadal differences appeared to be related to large-scale climate changes in the North Pacific. Catches of most taxa peaked in May–August, and were low during other months of the year. Several species were present for only part of the summer. Species composition of seine catches differed significantly between consecutive high and low tides, but not between consecutive sets or years. Midwater trawls took 26 species, 14 of which were present in Kachemak Bay, 19 near Chisik Island, and 7 at the Barren Islands. Community structures in shelf and nearshore waters were similar: diversity was high and abundance low at Chisik Island, whereas a few abundant species dominated at both Kachemak Bay and the Barren Islands. In addition, the low fish abundance near Chisik Island appeared to be related to declining seabird numbers at this colony.

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Dramatic changes in seabird and marine mammal populations in the Gulf of Alaska have been linked to shifts in abundance and composition of forage fish stocks over the past 20 years (Piatt and Anderson, 1996; Anderson et al.[1]). Coincident with cyclical fluctuations in seawater temperatures, abundance of several key forage species, including capelin (*Mallotus villosus*), pricklebacks (mostly *Lumpenella longirostris*), and Pacific sandfish (*Trichodon trichodon*) declined precipitously in the late 1970s. Meanwhile populations of large predatory fish, including walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), and several pleuronectids increased dramatically. Correspondingly, seabird diets shifted from mostly capelin in the 1970s to mostly Pacific sand lance (*Ammodytes hexapterus*) and juvenile pollock by the late 1980s (Piatt and Anderson, 1996). Furthermore, a variety of seabirds and marine mammals exhibited signs of food stress during the 1980s and early 1990s (Piatt and Anderson, 1996). Inferences about changes in Gulf of Alaska fish communities have been based on a limited number of site-specific long-term studies (e.g. Anderson et al.[1]); however, evidence is mounting that suggests these changes were wide-spread throughout the region (Francis et al., 1998).

The importance of inshore marine habitats as nursery areas for juveniles of many marine fish species has been well reported (Poxton et al., 1983; Orsi and Landingham, 1985; Bennett, 1989; Blaber et al., 1995; Dalley and Anderson, 1997). Studies in other parts of the world

[1] Anderson, P. J., S.A. Payne, and B. A. Johnson. 1994. Multi-species dynamics and changes in community structure in Pavlof Bay, Alaska 1972–1992. Natl. Mar. Fish. Serv., NOAA, Kodiak, Alaska. Unpubl. manuscript, 26 p.

have also described seasonal variation in shallow water fish assemblages (e.g. Horn, 1980; Allen, 1982; Nash and Gibson, 1982; Nash, 1988; Bennett, 1989). Little is known, however, about annual, seasonal, and daily variation in fish abundance in Alaska. Understanding the responses of fish populations at this scale are critical for examining finer-scale processes such as trophic interactions. Responses at these time scales also put interdecadal changes into perspective, and it is changes at the decadal scale that are rapidly becoming the focus of fishery oceanographers (Francis et al., 1998).

Our primary objectives were to assess variability in abundance, diversity, and distribution of nearshore fishes in three oceanographically distinct locations within lower Cook Inlet and to compare these data with information collected by Blackburn et al. (1980) 20 years ago. Until our study, Blackburn et al.'s 1976 surveys provided the only comprehensive description of nearshore fish communities in the region. Concurrent sampling of offshore species with midwater trawls also allowed us to make comparisons between shelf and nearshore fish communities.

Methods

Study sites

Lower Cook Inlet (Fig. 1), in south-central Alaska, is the largest embayment in the northern Gulf of Alaska. The area supports several important seabird colonies and numerous marine mammals, as well as important commercial and recreational fisheries for salmon (*Oncorhynchus* spp.) and Pacific halibut (*Hippoglossus stenolepis*). We studied three lower Cook Inlet areas that primarily support colonies of fish-eating common murres (*Uria aalge*) and black-legged kittiwakes (*Rissa tridactyla*): Gull Island, in Kachemak Bay; Chisik Island, on the western side of Cook Inlet; and the Barren Islands, near the entrance to Cook Inlet. Investigations of nearshore fish communities were initiated around these colonies to provide information that can be used to improve understanding of how forage fish abundance and distribution may influence seabird diets and productivity in these areas.

Kachemak Bay (Fig. 1) lies along the southeastern shore of Cook Inlet. The bay is 38 km wide at its entrance and 62 km long. The upper 6 km consists of mud flats that are exposed during low tide. Depths are relatively shallow, ranging from about 35 to 90 m, with some deeper areas (100 to 165 m) present off Gull Island along the south-central side of the bay. Water entering the bay originates from the Gulf of Alaska and is largely oceanic (Fig. 1; Burbank, 1977).

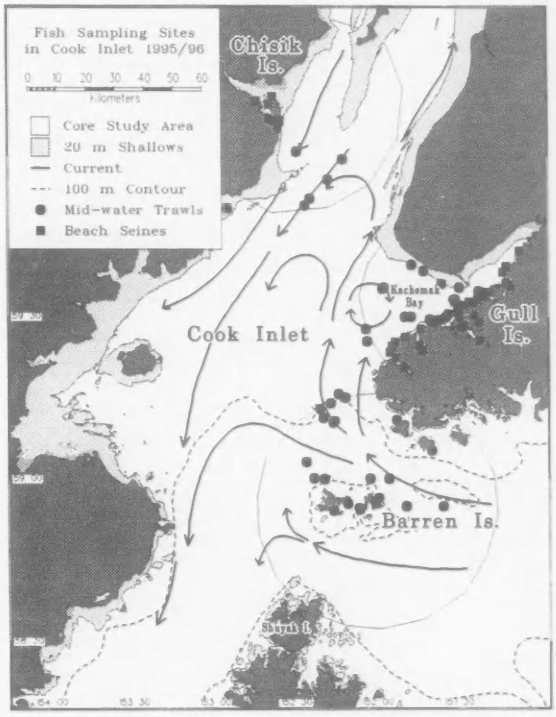

Figure 1

Map of lower Cook Inlet showing the three study areas, prevailing currents, bathymetry, and both beach seine and midwater trawl locations.

Chisik Island, on the western side of Cook Inlet (Fig. 1), is located in the mouth of Tuxedni Bay, which receives freshwater from glacier-fed rivers. Water passing outside the island is also estuarine, because it receives significant glacier-fed freshwater input from large rivers at the head of Cook Inlet before circulating down the western side of the inlet (Burbank, 1977; Feely and Massoth, 1982). Nearshore habitats around Chisik Island contain few sandy substrates and consist primarily of glacial silt and mud flats interspersed with rocky substrates that are exposed at low tides.

The Barren Islands, near the entrance to Cook Inlet (Fig. 1), are situated in a transition zone between deep Gulf of Alaska waters and the shallow Cook Inlet estuary. The Alaska Coastal Current enters Cook Inlet north of the Barren Islands, leading to intense upwelling of cold, nutrient-rich waters onto the shallow southeastern Cook Inlet shelf (Burbank, 1977). Because of the upwelling and strong tidal action (second highest tidal range in North America), waters in this area are turbulent and well mixed.

Field collections

We used beach seines to sample nearshore fish communities. These nets effectively and nonselectively sample shallow, inshore waters with sandy or smooth bottoms (Cailliet et al., 1986). In Kachemak Bay, samples were obtained during 16 June–26 July 1995 and 8 February–10 December 1996. Weather and sea conditions prevented sampling in January and November 1996. Sampling at Chisik Island and the Barren Islands occurred during 3 July–17 August, and 26 June–8 September 1996, respectively.

Our variable-mesh nets were 44 m long. The middle 15.3-m-long, 4-m-deep section was made of 3-mm knotless nylon stretch mesh (sm), and the wings tapered to a depth of 2.3 m were constructed of 13-mm knotted sm nylon. Thirty meters of rope were attached to the ends for deployment. Blackburn et al. (1980) used similar-size seines to sample Kachemak Bay in 1976. Nets were set parallel to shore about 25 m from the beach as described by Cailliet et al. (1986). Samples were collected about every two weeks in Kachemak Bay during May–September, and once a month throughout the winter. Samples from Chisik Island and the Barren Islands were collected every two weeks for the duration of their field seasons. .

We sampled 38 Kachemak Bay sites that were seined by Blackburn et al. (1980) in 1976. At these sites, we made 60 and 245 sets during May–September of 1995 and 1996, respectively. In comparison, Blackburn et al. made 131 sets during May–September 1976. Raw data from the 1976 study were obtained from J. Blackburn, Alaska Department of Fish and Game (ADF&G), Kodiak, Alaska.

Sets were made at eight sites on the west side of Chisik Island. Twenty-three of these sets were made at high tide and seven at low tide (low tide sets were limited by deep mud in the subtidal zone). At the Barren Islands, 40 sets (18 at high tide and 22 at low tide) were made in Amatuli Cove.

Beach seining was conducted within one-hour windows on either side of high and low tides. To assess tidal influence on catch rates, seven sites in Kachemak Bay were seined regularly on consecutive high and low tides during periods of maximum tidal oscillation (about every 15 days). A single set usually provides good representation of species richness and dominant species rank (Allen et al., 1992). However, to assess variability of beach seine catches, two consecutive sets were made adjacent to each other at the seven sites intensively studied at each tidal stage. As a result, these sites were sampled four times on each day that seining occurred. Fish were sorted and counted by species. Owing to the key trophic role of sand lance in the Gulf of Alaska (Blackburn and Anderson, 1997), these fish were also separated into adult (age groups ≥1) and juvenile (age group 0) categories on the basis of otolith interpretations.

Midwater trawls were used to sample offshore shelf environments by using the ADF&G 22-m stern trawler RV *Pandalus* in July 1996. Forage fish were located with a Biosonics DT4000 digital echosounder (120 kHz), and significant targets were fished by using a modified herring trawl with a 50-m^2 opening. Mesh sizes diminished stepwise from about 5 cm in the wings to 1 cm at the codend. The codend was lined with 3-mm mesh and contained a collecting bucket. Trawls were monitored with a Furuno netsounding system. Tow duration ranged from 20 to 60 minutes depending on fish concentrations. Midwater trawls were not directly comparable to beach seines; trawls selectively sampled the pelagic zone, whereas beach seines unselectively sampled both pelagic and demersal zones.

Analyses

We calculated four indices to assess broad differences between sites and sampling periods. The Shannon-Wiener index (H') indicates diversity; it increases as both the species number (richness) and equitability of species abundance (evenness) increase (Pielou, 1977). To measure species "richness" in diversity, we used Margalef's index (D; Margalef, 1968), and to assess equitability of species abundance, we calculated Pielou's evenness function (J'; Pielou, 1977). Similarity between species lists from different sampling periods was tested by using Jaccard's similarity coefficient for presence and absence data (Boesch, 1977). All diversity calculations were based on numbers of individuals and were made with natural logs ($\log_e$). Species assemblages were compared statistically with the Mann-Whitney rank sum test.

Results

Interdecadal comparison of beach seine catches in Kachemak Bay: 1976 versus 1995–96

Beach seines were an efficient method of catching nearshore fish. Of the 305 sets made in Kachemak Bay during May–September in 1995 and 1996, only four failed to yield fish. A total of 155,991 fish comprising 50 species were caught in these seines (Table 1). Of these species, 35 were primarily represented by juvenile stages. All species found during winter were also present during summer. Sand lance were most numerous; they represented 71% of total individuals.

Table 1

Frequency of occurrence and catch-per-unit-of-effort (CPUE) by species caught in beach seines during 1976 (May 21–September 29) and 1995/96 (May 16–September 27).

			1976[1] (131 Sets)		1995–96 (305 Sets)			
Status	Common name	Scientific name	% Occurence	CPUE	% Occurrence	CPUE	Change in % Occurrence[2]	Change in CPUE[3]
Abundant								
>50% of sets in at least one of the time periods	Dolly varden	*Salvelinus malma*	51.1	6.03	46.6	5.36	=	=
	Pacific sand lance	*Ammodytes hexapterus*	40.5	248.02	50.8	363.28	=	=
	Great sculpin	*Myoxocephalus polyacanthocephalus*	32.8	0.92	56.7	1.59	=	=
Common								
10–50% of sets in at least one of the time periods	Pink salmon	*Oncorhynchus gorbuscha*	24.4	6.14	39.0	28.16	=	=
	Rock sole	*Pleuronectes bilineatus*	15.3	0.33	30.2	1.24	=	=
	Pacific herring	*Clupea pallasi*	14.5	35.62	17.4	64.94	=	=
	Pacific cod	*Gadus macrocephalus*	0.8	0.01	27.2	14.49	+++	+++
	Whitespotted greenling	*Hexagrammos stelleri*	10.7	0.25	17.0	0.68	=	=
	Tubenose poacher	*Pallasina barbata*	5.3	0.07	15.7	0.42	+	=
	Threespine stickleback	*Gasterosteus aculeatus*	13.0	0.27	6.2	0.14	--	=
	Chinook salmon	*Oncorhynchus tshawytscha*	12.2	2.20	5.6	0.25	--	=
	Surf smelt	*Hypomesus pretiosus*	11.5	1.36	4.9	0.16	--	=
	Silverspotted sculpin	*Blepsias cirrhosus*	0.8	0.01	13.8	0.51	+++	+
Occasional	Snake prickleback	*Lumpenus sagitta*	6.9	0.41	5.6	0.58	=	=
1–10% of sets in at least one of the time periods	Chum salmon	*Oncorhynchus keta*	3.1	0.06	7.5	2.58	++	++
	Saffron cod	*Eleginus gracilis*	1.5	0.02	8.9	1.71	+++	+
	Pacific staghorn sculpin	*Leptocottus armatus*	6.1	0.09	3.3	0.04	=	=
	Sockeye salmon	*Oncorhynchus nerka*	0.8	0.01	8.5	2.54	+++	++
	Pacific tomcod	*Microgadus proximus*	0.0	<0.01	9.2	2.16	+++	+++
	Crescent gunnel	*Pholis laeta*	2.3	0.04	4.9	0.19	+	=
	Starry flounder	*Platichthys stellatus*	3.8	0.05	2.6	0.15	=	=
	Pacific sandfish	*Trichodon trichodon*	0.0	<0.01	6.2	0.15	+++	+++
	Kelp greenling	*Hexagrammos decagrammus*	0.0	<0.01	4.6	0.15	?[4]	?[4]
	Buffalo sculpin	*Enophrys bison*	0.8	0.02	3.6	0.08	+++	=
	Slender eelblenny	*Lumpenus fabricii*	0.0	<0.01	4.3	0.88	+++	+++
	Masked greenling	*Hexagrammos octogrammus*	3.8	0.15	0.3	0.01	---	--
	Rock greenling	*Hexagrammos lagocephalus*	0.0	<0.01	3.6	0.15	?[4]	?[4]
	Lobefin snailfish	*Liparis greeni*	0.0	<0.01	3.3	<0.01	+++	+++
	Lingcod	*Ophiodon elongatus*	1.5	0.02	1.3	0.02	=	=
	Butter sole	*Pleuronectes isolepis*	1.5	0.02	1.3	0.01	=	=
	Walleye pollock	*Theragra chalcogramma*	0.0	0.00	2.6	4.62	+++	+++
	Coho salmon	*Oncorhynchus kisutch*	1.5	0.50	0.7	0.01	--	--
	Warty sculpin	*Myoxocephalus verrucosus*	0.0	0.00	2.0	0.04	+++	+++
	Sablefish	*Anoplopoma fimbria*	0.0	0.00	1.6	0.17	+++	+++
	Longsnout prickleback	*Lumpenella longirostris*	1.5	0.06	0.0	0.00	---	---
	Daubed shanny	*Lumpenus maculatus*	0.0	<0.01	1.3	0.02	+++	+++

continued

Pacific herring (*Clupea pallasi*), pink salmon (*Oncorhynchus gorbuscha*), walleye pollock, and Pacific cod accounted for 22% of the remaining individuals. Great sculpin (*Myoxocephalus polyacanthocephalus*), sand lance, and Dolly Varden (*Salvelinus malma*) were the most frequently caught species during 1995–1996, each occurring in over 40% of the samples.

Table 1 (continued)

Status	Common name	Scientific name	1976[1] (131 Sets) % Occurence	1976[1] (131 Sets) CPUE	1995/96 (305 Sets) % Occurrence	1995/96 (305 Sets) CPUE	Change in % Occurrence[2]	Change in CPUE[3]
Rare								
<1% of sets in both time periods	Flathead sole	*Hippoglossoides elassodon*	0.0	<0.01	1.3	0.02	+++	+++
	Northern rockfish	*Sebastes polyspinis*	0.8	<0.01	0.7	0.01	[5]	[5]
	Sawback poacher	*Sarritor frenatus*	0.8	<0.01	0.3	<0.01	[5]	[5]
	Soft sculpin	*Psychrolutes sigalutes*	0.0	<0.01	1.0	0.02	[5]	[5]
	Petrale sole	*Eopsetta jordani*	0.0	<0.01	1.0	0.04	[5]	[5]
	Prowfish	*Zaprora silenus*	0.0	<0.01	0.7	0.01	[5]	[5]
	Padded sculpin	*Artedius fenestralis*	0.0	<0.01	0.7	0.01	[5]	[5]
	Pacific halibut	*Hippoglossus stenolepis*	0.0	<0.01	0.7	0.01	[5]	[5]
	English sole	*Pleuronectes vetulus*	0.0	<0.01	0.7	0.01	[5]	[5]
	Capelin	*Mallotus villosus*	0.0	<0.01	0.3	<0.01	[5]	[5]
	Arctic shanny	*Stichaeus punctatus*	0.0	<0.01	0.3	<0.01	[5]	[5]
	Yellow Irish lord	*Hemilepidotus jordani*	0.0	<0.01	0.3	<0.01	[5]	[5]
	Ribbed sculpin	*Triglops pingeli*	0.0	<0.01	0.3	<0.01	[5]	[5]
	Smooth alligatorfish	*Anoplagonus inermis*	0.0	<0.01	0.3	<0.01	[5]	[5]
	Smooth lumpsucker	*Aptocyclus ventricosus*	0.0	<0.01	0.3	<0.01	[5]	[5]

[1] 1976 data also includes: 28% sets with unidentified sculpins and 25% sets with unidentified greenlings. Data from J. Blackburn (Alaska Dept. Fish and Game, Kodiak).

[2] Change in frequency of occurrence between 1976 and 1995–96 defined by = (<100% change in frequency), + or – (100–200% change), ++ or -- (200–300% change), or +++ or --- (>300 % change).

[3] Change in CPUE between 1976 and 1995/96 defined by = (values within an order of magnitude), + or – (values changed by one order of magnitude), ++ or -- (values changed by two orders of magnitude), and +++ or --- (values changed by at least three orders of magnitude).

[4] Unidentified greenlings in 1976 were a mix of rock and kelp greenlings.

[5] CPUE and frequency of occurrence were too small to infer change.

In 1976, a total of 39,927 fish comprising at least 28 species were collected from 131 seine sets (greenling, Hexagrammidae, and sculpins, Cottidae, were not always identified to species; Blackburn et al., 1980; Table 1). To compare these data statistically with 1995–96 information, sculpin and greenling were combined into two general categories. By number, sand lance (81%) and herring (12%) accounted for more than 93 % of the 1976 catch. Four of the five species that dominated 1976 catches also dominated the 1995–96 catches (sand lance, herring, Dolly Varden, and pink salmon), and sand lance and herring were the two most abundant fish caught during both study periods. In 1976, only four (0.01%) fish were gadids (3 saffron cod, *Eleginus gracilis*; and 1 Pacific cod). By 1995–96, gadids (Pacific cod; saffron cod; Pacific tomcod, *Microgadus proximus*; and walleye pollock) were more numerous on the basis of catch-per-unit-of-effort (CPUE, defined as catch-per-individual-seine) by 1–3 orders of magnitude and had increased in frequency of occurrence by more than 300% (Table 1). Furthermore, Pacific cod was a dominant species in the 1995–96 catches. Similar increases in CPUE or frequency of occurrence were apparent for sockeye and chum salmon (*O. nerka*, *O. keta*), three sculpin species (silverspotted sculpin, *Blepsias cirrhosus*; buffalo sculpin, *Enophrys bison*; warty sculpin, *Myoxocephalus verrucosus*), Pacific sandfish, two prickleback species (slender eelblenny, *Lumpenus fabricii*; daubed shanny, *L. maculatus*), lobefin snailfish (*Liparis greeni*), sablefish (*Anoplopoma fimbria*), and a flatfish species (*Hippoglossoides elassodon*). Marked declines only occurred in catches of masked greenling (*Hexagrammos octogrammus*), coho salmon (*O. kisutch*), and longsnout prickleback (*Lumpenella longirostris*). Differences between 1976 and 1995–96 catches were significant on the basis of change in CPUE (Mann-Whitney rank sum test; t=1339.5, P=0.007), percent composition (t=1373.0, P=0.018), and frequency of capture (t=1398.0, P=0.033).

Changes in fish abundance were accompanied by changes in community diversity (Table 2). The Shannon-Wiener index (H') was greater in 1995–96 than in 1976, reflecting the large increase in gadid species during the 1990s (accounting for two thirds of the difference in H'). Species richness (D) was also higher in 1995–96, compared with 1976. This difference resulted from the fact that four species represented 92% of the total 1995–96 catch. In contrast, only two species accounted for 93% of the 1976 catch.

Table 2

Catch-per-unit-of-effort (CPUE) and species diversity indices from nearshore and shelf areas of Kachemak Bay (1976 and 1995–96), Chisik Island, and the Barren Islands. Diversity indices: H' = species diversity; J' = species evenness function; D = species richness (see "Methods" section).

		CPUE		H'		J'		D	
Location	Year	Nearshore	Shelf	Nearshore	Shelf	Nearshore	Shelf	Nearshore	Shelf
Kachemak Bay	1976	305	—	0.74	—	0.23	—	2.27	—
Kachemak Bay	1995–96	511	345	1.05	1.07	0.29	0.40	3.26	1.51
Chisik Island	1996	33	92	2.13	1.89	0.67	0.64	3.34	2.85
Barren Islands	1996	4506	821	0.06	0.31	0.03	0.16	0.91	0.63

Table 3

Comparison of 1995 and 1996 Kachemak Bay beach seine catches for species that occurred in more than 10% of sets.

	1995			1996		
Species	Frequency of capture	Percent of total catch	CPUE	Frequency of capture	Percent of total catch	CPUE
Pacific sand lance	75.0	66.6	310.2	67.2	60.0	250.1
Dolly varden	68.3	1.8	8.5	55.7	1.8	7.5
Great sculpin	68.3	0.7	3.2	49.2	0.2	1.0
Pink salmon	51.7	3.0	14.0	52.5	13.8	57.4
Rock sole	33.3	0.2	1.0	36.9	0.4	1.5
Pacific cod	41.7	7.4	34.4	18.9	0.5	2.2
Pacific herring	30.0	16.1	75.1	11.5	16.5	68.8
Whitespotted greenling	20.0	0.2	0.9	21.3	0.1	0.5
Tubenose poacher	31.7	0.3	1.3	11.5	>0.1	0.2
Silverspotted sculpin	20.0	0.2	0.8	17.2	0.1	0.5

The low equitability (J') in both time periods reflected dominance by a few species (e.g. sand lance, herring) in catches.

Jaccard's similarity coefficient indicated only moderate (59%) similarity in the presence-absence of species between 1995–96 and 1976. This may have resulted from a combination of 1) a dramatic increase in abundance of some species in 1995–96 (e.g. tomcod, sandfish); and 2) increased fishing effort in 1995–96, which may have increased catches of less common species (e.g. prowfish, *Zaprora silenus*; capelin) that might have also been detected in 1976, if fishing effort had been greater.

Interannual comparison of beach seine catches in Kachemak Bay: 1995 versus 1996

As evidenced by catches of common species in Kachemak Bay (Table 3), there was little obvious difference in catches between consecutive years. During June and July of 1995, 27,944 fish belonging to 42 species were caught in 60 beach seine sets (CPUE=466). During the same period in 1996, 50,859 fish representing 37 species were found in 122 sets (CPUE=417). Forty-four species were identified over the course of the two year study, of which 30 were caught in both years. Species diversity (H') was similar in 1995 and 1996 (1.21 and 1.22, respectively), as were species richness (D; 3.61 and 3.43, respectively) and equitability (J'; 0.34 in both years).

Jaccard's similarity coefficient indicated a 68% similarity between the species assemblages caught in 1995 and 1996. Species not represented in one year or the other were generally uncommon species that were found in only a few seine sets. Differences in percent composition of 1995 and 1996 species assemblages were not significant (Mann-Whitney rank sum test).

Seasonal variation in the nearshore fish community of Kachemak Bay

To examine seasonal variation in nearshore fish abundance, we used only data collected in 1996 (130,325 fish, 46 species, 283 beach seine sets in February–December). Most species were present in greatest numbers during summer months, apparently moving inshore as water temperatures increased above 4°C in May (Fig. 2), and moving offshore as temperatures declined in October (Fig. 3). Almost no fish were caught or observed during the winter months (December–March; Fig. 3); however, CPUE increased markedly for all species in June and declined dramatically in mid-July. This pattern was also reported by Blackburn et al. (1980; Fig. 4). This change largely resulted from changes in nearshore sand lance abundance but was compounded by movements of pink salmon and Pacific cod. Large catches of juvenile pink salmon increased the CPUE in June as they migrated along shorelines (Orsi and Landingham, 1985), but salmon CPUE declined rapidly in July as fish moved offshore (Fig. 3; Blackburn et al., 1980). Catches of gadids (particularly Pacific cod and pollock) increased markedly in late summer (Fig. 3) and contributed to the large August increase in CPUE. However, most of the August–September increase in CPUE was due to recruitment of first-year sand lance (Fig. 3), which dominated late summer seine catches after adults moved out of nearshore environments in late July (Blackburn et al., 1980). In October, adult sand lance returned to inshore waters to spawn (Dick and Warner, 1982; Robards, 1999). CPUE began declining rapidly in October, in conjunction with a decline in diversity from 34 species in August to only 3 by December.

Figure 2

Seasonal variation in 1996 subsurface temperatures (5 m below low tide [0 m]) at Kachemak Bay (1), Chisik Island (2), and the Barren Islands (3).

We also observed strong seasonal trends in use of nearshore habitats by other species. Dolly Varden moved into nearshore waters in April, where they remained throughout July. After July they followed salmon into natal freshwater systems to overwinter (Isakson et al., 1971, Orsi and Landingham, 1985). Juvenile rock sole (*Pleuronectes bilineatus*) and great sculpins were consistently the most abundant fish found in nearshore habitats during February–March. Flatfish (Pleuronectidae) were caught at low rates throughout spring and summer but were not present after October (Fig. 3). Numbers of juvenile great sculpins increased rapidly in spring owing to an influx of small juveniles (<20 mm). Catches of these juveniles fell markedly by late June, and small but regular numbers of second-year individuals were caught during summer. Only one capelin was caught in Kachemak Bay (26 July 1995) prior to October 1996, when 1586 first-year fish were captured in three seine sets. Several large capelin schools were also observed at the same time. Capelin were also captured in three of eight seine sets in December. Although herring were present throughout the summer (Fig. 3), almost all of them (99%) were captured in five June and four August sets at one area (Halibut Cove) historically known for its aggregations of herring (Rounsefell, 1930).

Species abundance, diversity (H'), and richness (D) in the nearshore Kachemak Bay fish community increased steadily from April to June, peaked in July, and declined rapidly in September. Although sand lance dominated the community in summer, more than 30 species of fish were present during June–August. Species evenness (J') declined throughout summer, when sand lance dominated nearshore habitats, but increased again in fall as numbers of species and individuals declined.

Variability among consecutive beach seine sets and tidal states in Kachemak Bay

To assess variability in catches among sets and tidal states within Kachemak Bay, we made two sets immediately adjacent to each other at each site during consecutive high and low tides (i.e. 4 sets per site, 17 samples, 68 sets). CPUE declined markedly between first and second sets at both high (42% decline) and low (50% decline) tides, although numbers of species caught remained similar (Table 4). Jaccard's similarity coefficient for species composition indicated a high degree of similarity between the two adjacent high (75%) and low (74%) tide sets. However, species

diversity, richness, and evenness all increased on the second set, at both tidal states, because of a decrease in dominant species (Table 4). Because species composition of seine catches did not differ significantly between consecutive sets at high and low tidal states (Mann-Whitney rank sum test), it appears that one set is adequate for assessing species richness and dominance, as suggested by Allen et al. (1992)

Twenty-eight species were represented in high tide sets and the overall CPUE was 425, in contrast to 38 species and a CPUE of only 191 at low tide. This difference probably resulted from a scarcity of pricklebacks (Stichaeidae), gunnels (Pholidae), and sculpins at high tide. The species difference in catches in part accounted for the moderate coefficient of similarity (Jaccard's) between tidal states (58% and 61% on sets 1 and 2, respectively). Catch composition differed significantly between high and low tides (Mann-Whitney rank sum test; T=2645, P=0.02). Several schooling species (e.g. pink salmon, adult sand lance) and one demersal species (great sculpin) showed little disparity in overall CPUE or frequency of occurrence between tidal states (Table 5). These species (or age classes) appeared to remain close to the shore throughout the tidal cycle. Other species (e.g. Dolly Varden, juvenile sand lance) apparently moved from deeper waters into the intertidal zone at high tide, as shown by the greater frequency of capture and CPUE. Although Pacific cod, saffron cod, whitespotted greenling (*Hexagrammos stelleri*), silverspotted sculpin, juvenile great sculpin, and rock sole were caught at both tide levels, these species appeared to remain preferentially in the subtidal zone during high tide (Table 5). Overall, species diversity, richness, and evenness were greatest at low tides (Table 4).

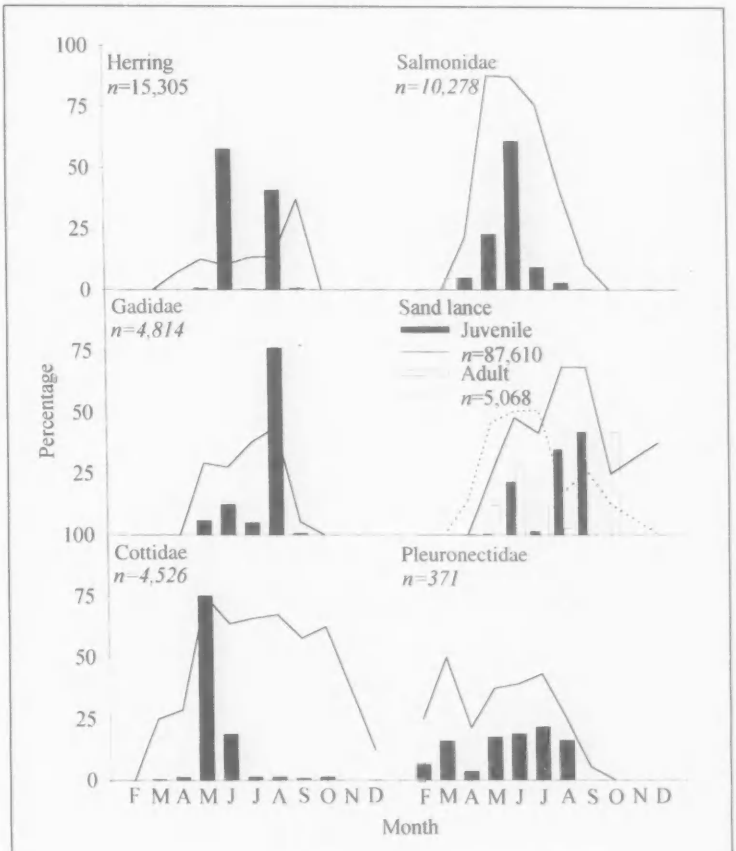

Figure 3

Seasonal variation in CPUE (bars) and frequency of occurrence (lines) of selected fish species caught by beach seines in Kachemak Bay.

Geographic comparison of beach seine catches from Kachemak Bay, Chisik Island, and the Barren Islands

A total of 988 fish representing 24 species were caught in 30 beach seine sets in the warmer (Fig. 2) nearshore waters around Chisik Island during summer 1996 (Table 6). Dolly Varden was the most common species; it was present in 63% of the sets and represented 30% of total catch by numbers. In contrast to Kachemak Bay and the Barren Islands, sand lance were found in only 33% of sets and accounted for only 24% of the catch by number. Snake prickleback (*Lumpenus sagitta*; 12%) and Pacific cod (8%) were the next most abundant species. Sculpins and flatfishes were also commonly caught in the sets.

A total of 180,232 fish representing at least 12 species (including 482 unidentified sculpins, 1 unidentified flatfish, and 1 unidentified greenling) were caught in 40 seine sets in the somewhat cooler (Fig. 2) nearshore waters at the Barren Islands during summer 1996 (Table 6). Barren Islands catches were dominated by sand lance (predominantly juveniles; Table 6). This species was found in 90% of the sets and represented over 99% of the total catch. Other species commonly found in the sets included Pacific

cod (>50%), sculpins (>40%), and butter sole (*Pleuronectes isolepis*; 18%).

CPUE varied by about two orders of magnitude among the three areas. On the basis of this variable, we determined that Barren Islands waters were more productive than those of Kachemak Bay and Chisik Island (Table 2). However, Chisik Island and Kachemak Bay displayed greater species diversity and richness than the Barren Islands (Table 2; Fig. 5). Equity (J') was much greater at Chisik Island (Table 2), indicating that this community was not dominated by any one species. Jaccard's similarity coefficients were low when compared between areas. Species assemblages in Kachemak Bay and at Chisik Island were similar (42%), and both of these areas differed from the Barren Islands (<25% similarity).

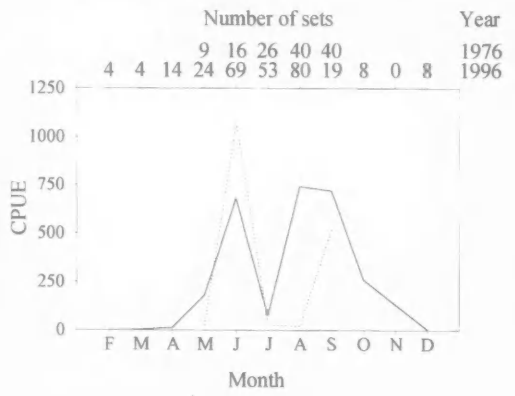

Figure 4

Seasonal variation of CPUE in beach seines during 1976 (·····) and 1996 (——) in Kachemak Bay.

Comparison of nearshore and shelf communities in lower Cook Inlet

In 1996, midwater trawls were made during July at all three study sites (Fig. 1). Nine species were found

Table 4

Catch-per-unit-of-effort (CPUE) and species diversity indices for consecutive beach seine sets made at high and low tides in Kachemak Bay. Diversity indices: H' = species diversity; D = species richness; J' = species evenness function (see "Methods" section).

Tidal state	Set	CPUE	Species	H'	D	J'
High	1	539.35	24	0.85	2.34	0.27
High	2	310.97	25	1.42	2.59	0.44
High	Overall	425.16	28	1.09	2.63	0.33
Low	1	255.26	33	1.96	3.53	0.56
Low	2	127.71	33	2.29	3.82	0.65
Low	Overall	191.49	38	2.17	3.91	0.60

Table 5

Frequency of occurrence and catch-per-unit-of-effort (CPUE) of selected fish species (occurring in more than 10% of sets) caught on consecutive beach seine sets made at high and low tide in Kachemak Bay.

	High tide				Low tide			
	Set 1 (34 sets)		Set 2 (34 sets)		Set 1 (34 sets)		Set 2 (34 sets)	
Species	% Occurrence	CPUE	% Occurrence	CPUE	% Occurrence	CPUE	% Occurrence	CPUE
Pink salmon	47.1	77.6	38.2	44.5	44.1	41.68	38.2	24.24
Dolly varden	47.1	3.09	47.1	14.85	29.4	1.65	32.4	2.26
Pacific cod	8.8	3.24	11.8	6.32	29.4	22.82	26.5	18.85
Saffron cod	5.9	0.06	2.9	0.74	14.7	4.88	14.7	7.82
Juvenile sand lance	44.1	417.94	61.8	187.32	32.4	88.97	32.4	9.79
Adult sand lance	35.3	8.74	32.4	16.4	41.2	24.76	38.2	2.00
Whitespotted greenling	8.8	0.15	2.9	0.03	20.6	0.32	23.5	2.06
Silverspotted sculpin	0.0	0.00	5.9	0.12	26.5	2.06	29.4	0.59
Juvenile great sculpin	8.8	5.88	5.9	15.24	26.5	46.59	23.5	33.74
Adult great sculpin	41.2	0.94	52.9	1.53	58.82	1.91	44.12	0.85
Tubenose poacher	2.9	0.03	2.9	0.09	8.8	0.18	11.8	0.32
Rock sole	2.9	0.03	11.8	0.12	58.8	3.32	50.0	2.59

(Table 7) that were not present in any of the beach seine sets (Tables 1 and 6). Similar proportions of the most abundant taxa were evident in trawl and beach seine samples from Kachemak Bay (Fig. 5), and sand lance dominated both nearshore and offshore catches. Few midwater trawls were made at Chisik Island because acoustic sign signals rarely indicated that fish were present in the water column. There was moderate overlap in composition of seine and trawl catches at Chisik Island, and no single species dominated the samples (Fig. 5). In contrast, the shelf environment of the Barren Islands was clearly dominated by walleye pollock, and nearshore habitats were almost completely populated by sand lance.

CPUE (defined as catch-per-individual-trawl) for trawl sets varied by an order of magnitude among the three study areas, paralleling results from beach seine sets (Table 2). Geographic trends in community diversity indices from trawl catches were also similar to those calculated for nearshore beach seine sets (Table 2). Species diversity (H'), species richness (D), and equity (J') were highest at Chisik Island, somewhat lower in Kachemak Bay, and lowest at the Barren Islands (Fig. 5).

Table 6

Frequency of occurrence and catch-per-unit-of-effort (CPUE) by species for beach seine catches at Chisik Island (30 sets) and the Barren Islands (40 sets) in 1996.

	Chisik Island (988 fish)		Barren Islands (180,232 fish)	
Common name[1]	% Occurrence	CPUE	% Occurrence	CPUE
Pacific sand lance	33.3	7.77	90.0	4465.03
Pacific cod	16.7	2.47	52.5	12.58
Dolly varden	63.3	9.90	2.5	0.13
Great sculpin	50.0	1.07	0.0	0.00
Pink salmon	13.3	0.70	35.0	11.23
Starry flounder	46.7	1.70	0.0	0.00
Unidentified sculpins	0.0	0.00	42.5	12.05
Snake prickleback	33.3	3.97	0.0	0.00
Capelin	13.3	0.43	10.0	3.38
Threespine stickleback	23.3	0.33	0.0	0.00
Butter sole	0.0	0.00	17.5	0.33
Rock sole	16.7	2.07	0.0	0.00
Lingcod	0.0	0.00	15.0	0.33
Whitespotted greenling	13.3	0.73	0.0	0.00
Crescent gunnel	10.0	0.37	0.0	0.00
Kelp greenling	0.0	0.00	7.5	0.13
Pacific herring	6.7	0.60	0.0	0.00
Eulachon	6.7	0.10	0.0	0.00
Silverspotted sculpin	6.7	0.07	0.0	0.00
Padded sculpin	6.7	0.07	0.0	0.00
Pacific staghorn sculpin	6.7	0.07	0.0	0.00
Sawback poacher	6.7	0.17	0.0	0.00
Rock greenling	3.3	0.03	2.5	0.03
Surf smelt	0.0	0.00	5.0	0.55
Coho salmon	3.3	0.03	0.0	0.00
Sockeye salmon	3.3	0.03	0.0	0.00
Longfin smelt	3.3	0.17	0.0	0.00
Pacific tomcod	3.3	0.07	0.0	0.00
Pacific halibut	3.3	0.03	0.0	0.00
Walleye pollock	0.0	0.00	2.5	0.03

[1] Latin names included in Table 1 except eulachon (*Thaleichthys pacificus*) and longfin smelt (*Spirinchus thaleichthys*).

Table 7

Total numbers of fish by species caught in midwater trawls in shelf waters within about 40 km of Gull Island (Kachemak Bay), Chisik Island, and the Barren Islands in 1996.

Common name	Scientific name	Kachemak Bay 16 Sets	Chisik Island 6 Sets	Barren Islands 17 Sets
Walleye pollock	*Theragra chalcogramma*	456	123	12,912
Pacific sand lance	*Ammodytes hexapterus*	3857	132	195
Capelin	*Mallotus villosus*	441	141	840
Pink salmon	*Oncorhynchus gorbuscha*	413	44	0
Pacific cod	*Gadus macrocephalus*	317	4	1
Pacific sandfish	*Trichodon trichodon*	0	59	0
Chinook salmon	*Oncorhynchus tshawytscha*	0	19	0
Tadpole sculpin	*Psychrolutes paradoxus*	16	0	0
Snailfish	*Cyclopteridae*	1	4	0
Eulachon	*Thaleichthys pacificus*	0	10	0
Prowfish	*Zaprora silenus*	9	0	1
Rock sole	*Pleuronectes bilineatus*	2	1	6
Flatfish	*Pleuronectidae*	6	0	0
Armorhead sculpin	*Gymnocanthus galeatus*	0	5	0
Sculpin	*Myoxocephalus* spp.	2	0	1
Sculpin	*Gymnocanthus* spp.	2	0	0
Dover sole	*Microstomus pacificus*	0	2	0
Poacher	*Bathyagonus* spp.	2	0	0
Smooth alligatorfish	*Anoplagonus inermis*	0	2	0
Pacific herring	*Clupea pallasi*	0	1	0
Spinyhead sculpin	*Dasycottus setiger*	0	1	0
Northern sculpin	*Icelinus borealis*	0	1	0
Ribbed sculpin	*Triglops pingeli*	0	1	0
Arrowtooth flounder	*Atheresthes stomias*	0	1	0
Starry flounder	*Platichthys stellatus*	1	0	0
Pacific lamprey	*Lampetra tridentata*	0	1	0
Total fish		5525	552	13,956

Discussion

Nearshore fish communities

The overall composition of beach seine catches did not differ between 1995 and 1996, and community indices were also similar between years. This gives us confidence that changes in community composition observed between 1976 and 1995–96 reflected decadal-scale variability rather than just annual variability. The increase in beach seine CPUE between 1976 and 1995–96 may have also been real, but we have less confidence in this result because beach seines were deployed closer to shore in 1976 (10 m) than in 1995–96 (25 m), and this difference might have influenced catch rates. The most dramatic difference between decades was in catches of gadids (including pollock). Few were caught in the whole of lower Cook Inlet during 1976, when gadids represented only 0.2% of the total catch (85 individuals in 262 seines; Blackburn et al., 1980). The 1000-fold increase in gadids that we observed in the mid-1990s parallels a similar increase in abundance of gadids in offshore shrimp trawls in Cook Inlet (Bechtol, 1997) and the Gulf of Alaska (Piatt and Anderson, 1996; Anderson et al., 1997). Similarly, the increase in pleuronectids and salmonids that we observed in Kachemak Bay between 1976 and 1995–96 was paralleled in the Gulf of Alaska in shrimp trawls (Anderson et al., 1997) and commercial salmon catches (Francis and Hare, 1994), respectively.

Interdecadal changes in abundance of these fishes are probably related to large-scale climate changes in the North Pacific, but causal mechanisms are unclear (Francis et al., 1998). Water temperatures in the northern Gulf of Alaska changed from being

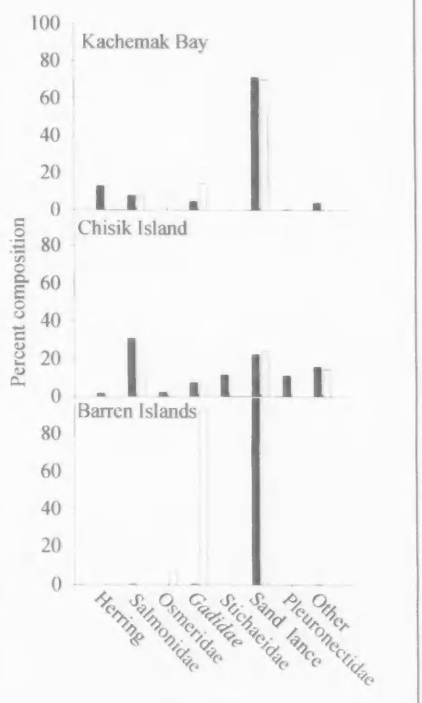

Figure 5

Species composition (% of total catch) in the nearshore (■) and shelf (□) areas of Kachemak Bay, Chisik Island, and the Barren Islands.

colder than average through the 1970s to warmer than average through the 1980s and 1990s (Royer, 1993). Temperature changes have been linked to El Niño Southern Oscillation (ENSO) events and shifts in the location and intensity of the Aleutian low-pressure cell (Niebauer, 1983). This climatic "regime shift" caused a major reorganization of North Pacific biota (Francis et al., 1998). Phytoplankton and zooplankton abundance increased in the Gulf of Alaska, and this may have increased availability of food to larval stages of salmon and other groundfish, leading to enhanced recruitment (Francis et al., 1998). The timing of peak production of zooplankton biomass also changed, and this may have influenced recruitment in a suite of fish and invertebrates by altering the survival of larvae ("match-mismatch" hypothesis; Anderson and Piatt, in press). However, not all species appear to have been affected by changing climate. It is notable that the most abundant fish in Kachemak Bay, sand lance, exhibited no significant change in abundance or frequency of occurrence between 1976 and 1995–96. Sand lance have a unique life history. They spawn during the fall and larvae emerge in January or February, much earlier than the spring plankton blooms or larvae of many other Gulf of Alaska fish species. This strategy may be adaptive in situations where prey availability is unpredictable (Haldorson et al., 1993). Therefore, sand lance recruitment may have been little affected by changes in the timing or magnitude of zooplankton abundance during spring and early summer.

Capelin abundance declined sharply throughout the Gulf of Alaska after the late 1970s (Bechtol, 1997; Piatt and Anderson, 1996) but may have started to rebound in Cook Inlet waters during the early 1990s (Roseneau et al.[2]). Apart from catches in 10 beach seine sets (three sets in Kachemak Bay and at Chisik Island, and four at the Barren Islands), there is little evidence that capelin occur in nearshore areas of Cook Inlet. However, they were the third most common species caught in midwater trawls, and capelin were widely consumed by halibut and seabirds in Cook Inlet in 1995 and 1996 (Roseneau and Byrd, 1997; Roseneau et al.[3]). This species may occupy habitats offshore of the littoral zone, but largely inshore of where we made midwater trawls and may therefore be under-represented by this study.

The diversity of species in Kachemak Bay is comparable to that of other subarctic areas of Alaska. Isakson et al. (1971) caught 40 species in the nearshore waters of Amchitka Island and Orsi and Landingham (1985) found 42 species in southeastern Alaska. About 20–30 species are typically present in nearshore habitats in the more temperate regions of Sweden (Thorman, 1986a), Norway (Nash, 1988), Scotland (Gibson et al., 1996), and California (Allen and Horn, 1975; Horn, 1980; Allen, 1982).

In Kachemak Bay, four species accounted for over 92% of the catch in 1995–96, and two species represented over 93% of the 1976 catch. One species (sand lance) made up more than 99% of Barren Islands catch, and even at Chisik Island, where species equity was high, only five species accounted for 79% of the total numbers. As might be expected from these patterns of relative abundance, these fish were predominantly juveniles (Gibson et al., 1996) and typically low in the trophic web (Allen, 1982). In estua-

[2] Roseneau, D. R., A. B. Kettle, and G. V. Byrd. 1995 and 1996. Common murre restoration monitoring in the Barren Islands, Alaska. 1993 and 1994. Exxon Valdez Oil Spill Restoration Projects 93049 and 94039. Unpubl. final reports.

[3] Roseneau, D. G., A. B. Kettle, and G. V. Byrd. 1996 and 1997. Barren Islands seabird studies. *In* D. C. Duffy (compiler), APEX: Alaska Predator Ecosystem Experiment. Exxon Valdez Oil Spill Restoration Project. Alaska Natural Heritage Program, University of Alaska, Anchorage. Appendix J. Unpubl. annual reports.

rine, inshore, and bay habitats in the northeastern Pacific, it appears to be normal for five or fewer species to account for more than 75% of the individuals in local fish communities, even though the total number of species comprising these communities may be much larger (e.g. Allen and Horn, 1975; Hancock, 1975; Horn, 1980; Allen, 1982; Gordon and Leavings, 1984; Orsi and Landingham, 1985).

Although no significant differences were observed in species composition between consecutive beach seine sets at the same study sites, CPUE was markedly reduced for the second sets made at both high and low tides. This reduction in CPUE may have resulted from avoidance by schooling species to disturbance, or removal of most individuals during the first set. As Gibson et al. (1996) observed, we found marked differences in species composition between tidal states, and the number of species found at low tide was reduced by 26% in sets made at high tide. The fact that only species that typically migrate into the intertidal zone (e.g. pink salmon, sand lance, great sculpin) were caught at high tide may have accounted for this difference. Juvenile sand lance occurred in greater numbers and were caught at higher frequencies during high and flood tides, compared with low and ebb states as observed by Blackburn and Anderson (1997). These results suggested that juvenile sand lance may have moved laterally on each tide, by ascending from demersal habitats to pelagic zones at flood stages, and returning at ebb stages. Larval plaice *(Pleuronectes platessa)* of the North Sea exhibited this kind of behavior in coastal nursery areas (Rijnsdorp et al., 1985).

High-latitude fish assemblages, particularly those found in shallow water habitats, are subject to large seasonal variations in temperature and day length. These physical factors impart a strong natural seasonality to community structure (Nash, 1988) as observed in the nearshore waters of Kachemak Bay. Some fish species move from shallow water habitats to deeper waters in winter when thermal tolerances are exceeded (Allen and Horn, 1975; Allen, 1982; Bennett, 1989). Decreases in catch size between spring and fall peaks have also been observed by many investigators (e.g. Livingston, 1976; Horn, 1980; Allen, 1982; Thorman, 1986b; Methven and Bajdik, 1994). However, the midsummer CPUE declines in Kachemak Bay were not accompanied by declines in species diversity, as observed by Thorman (1986b). Reduction in numbers of adult Atlantic sand lance (*Ammodytes marinus*) has also been noted in midsummer seabird diets (Monaghan et al., 1996). This change corresponds to the time when predation by chick-rearing seabirds is at maximum; adult sand lance may be responding to the increased presence of predators by avoiding nearshore and surface habitats, or they may be coincidentally estivating in preparation for spawning (Sekiguchi et al., 1976).

Geographic variability

The relative abundance and distribution of fish species in lower Cook Inlet appears to be largely determined by oceanography and sediment influx. Intense insular upwelling of nutrient-rich waters around the Barren Islands leads to high productivity along frontal zones that in turn results in high abundance of fish. Upwelled water entering Kachemak Bay is nutrient-rich and becomes locally stratified, resulting in the highest primary production recorded in lower Cook Inlet (Larrance et al., 1977). In Kachemak Bay, high habitat diversity and the plankton prey-base provide the marine environments needed to support an abundant, diverse fish community. As water circulates around Cook Inlet to Chisik Island (Fig. 1), sediment loads increase from freshwater glacial runoff (Feely and Massoth, 1982), leading to maximum primary production that is only about one-tenth of that found in Kachemak Bay (Larrance et al., 1977). The lower abundance of sand lance at Chisik Island probably results from a combination of low food availability and deposition of glacial silt and mud (Feely and Massoth, 1982) that blanket most of the local substrates. Sand lance are known to require clean, sandy nearshore substrates (e.g. Pinto et al., 1984), and they appear to favor these habitats; few were caught in the offshore, oceanic waters surrounding the Barren Islands. On the north side of the Alaska Peninsula, sand lance also dominated nearshore catches and were caught less frequently offshore (Houghton, 1987).

The storm-prone Barren Islands displayed lower species diversity than the other lower Cook Inlet areas. Species inhabiting this more exposed oceanic region may avoid shallow habitats and favor slightly deeper, less disturbed waters (Thorman, 1986a), leading to reduced nearshore diversity (Horn, 1980). Diversity of fish in the nearshore Kachemak Bay and Chisik Island environments was apparently related to increasing habitat diversity and reduced salinity, as seen elsewhere (Thorman, 1986b; Blaber et al., 1995).

The most notable difference observed between nearshore and offshore shelf environments in lower Cook Inlet was that shelf areas were dominated by walleye pollock. Pollock were found in 88% of midwater trawls, compared with only 3% in beach seine sets. This species does not appear to use nearshore habitats as nursery areas, as does a related species, the Pacific cod (Houghton, 1987). The presence of some pollock in nearshore areas of Kachemak Bay may be related in part to the pres-

ence of oceanic water within the bay. Pollock also frequent Amchitka Island nearshore environments, which are similarly bathed by mixed, oceanic waters (Isakson et al., 1971).

Unequivocal declines in seabird populations (predominantly murres and black-legged kittiwakes) at Chisik Island (Slater et al., 1994) may be related to declines of locally abundant forage fish, particularly sand lance. It is possible that historically larger numbers of capelin (Piatt and Anderson, 1996) or herring (or both) (Rounsefell, 1930; Reid, 1971) may have inhabited this region when stocks of pelagic seabirds were higher prior to the mid-1970s. Colder than average temperatures prior to the late 1970s would have favored both of these fish species (Ware, 1995; Frank et al., 1996).

Limitations of the study

Sampling nearshore habitats with beach seines was limited to sandy and cobble substrates. Strong currents or inshore swells over 0.5 m also prevented effective retrieval of nets. Therefore, fish inhabiting muddy or rocky substrates, mussel (*Mytilus edulis*) and kelp beds, or the surf zone are under-represented in our study. The surf zone is preferentially used by some species because of low numbers of predators and food-rich waters (Bennett, 1989).

Burrowing fish, such as sand lance, may also be under-represented in the beach seine data because of their ability to escape under the net (Dick and Warner, 1982; Gordon and Leavings, 1984; Allen et al., 1992; Robards, personal obs). However, sand lance were the most abundant fish caught in Kachemak Bay and the Barren Islands, indicating that beach seines were clearly effective for sampling this species.

Juvenile cod migrate from deep water habitats during the day to shallower, nearshore waters at night (Methven and Bajdik, 1994; Gibson et al., 1996). Therefore, cod and other gadids may be under-represented in our catches, which were made only during daylight hours. However, diel variability in gadid catches has been shown to be lower than variability associated with tide cycles (Gibson et al.,1996).

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Mortality estimates and demographic analysis for the Australian sharpnose shark, *Rhizoprionodon taylori*, from northern Australia

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Abstract.—Natural mortality was estimated for *Rhizoprionodon taylori* by using seven indirect methods based on relationships between mortality and life history parameters and one direct method, catch curve analysis. Estimated values from indirect methods were 0.60 to 1.65, whereas catch curves produced values of 0.56 for females and 0.70 for males. Demographic analysis was undertaken by using standard life history table techniques. Life history tables where each of the seven indirect estimates of natural mortality for *R. taylori* produced intrinsic rates of natural increase from −1.297 to 0.212 for an unfished population, and only two of the seven produced positive population growth. The implications of these results are discussed in relation to the accuracy of indirect methods for estimating natural mortality for *R. taylori* and other species of shark. The catch curve method was considered the best estimate of natural mortality and gave an intrinsic rate of increase of 0.27 and a doubling time of 2.55 years. The results of life history table analysis with the estimate of natural mortality from the catch curve analysis indicated that a *R. taylori* population could sustain fishing mortality up to 0.18 if applied evenly over all age classes, or 0.67 if age at first capture was two years. The implications of this study are discussed in relation to sustainability of elasmobranch stocks, particularly short-lived, fast growing, early maturing species.

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In a paper entitled "Problems in the rational exploitation of elasmobranch populations and some suggested solutions," Holden (1974, p. 137) concluded that "elasmobranch stocks offer very limited opportunities for long-term exploitation." Holden's conclusion was based on the fact that elasmobranch life history traits, such as slow growth, long lifespan, late age at maturity, and low fecundity, make populations very susceptible to recruitment overfishing. Holden's hypothesis has been supported by evidence from a number of shark stocks that have been rapidly overfished. These stocks include the spiny dogfish off Scotland and Norway (*Squalus acanthias*; Holden, 1968, 1977), the soupfin shark off California (*Galeorhinus galeus*; Ripley, 1946), the basking shark of the Irish Sea (*Cetorhinus maximus*; Parker and Stott, 1965), the porbeagle of the western Atlantic (*Lamna nasus*; Casey et al., 1978), and the sandbar and dusky sharks of the western North Atlantic (Musick et al., 1993). The majority of these examples are long-lived, slow growing, late maturing, temperate-water species. This group of commonly cited examples does not, however, represent the full range of elasmobranch life history traits and as such represents a biased set of data on which to base conclusions about sustainability of elasmobranch stocks. In particular, the examples lack representatives from tropical areas, especially short-lived, rapidly growing, early maturing species. With adequate information on species with a wide range of life histories, a more accurate assessment of the ability of elasmobranch stocks to sustain fishing pressure should be possible.

In recent years the use of demographic analysis (i.e. life history tables) has become popular in the assessment of elasmobranch populations and their ability to be sustainably fished (e.g. Hoenig and Gruber, 1990; Cailliet, 1992; Cailliet et al., 1992; Cortes, 1995; Cortes and Parsons, 1996; Sminkey and Musick, 1996; Au and Smith, 1997; Cortes, 1998). This style of analysis requires only knowledge of the life history traits of a species. Because demographic models are static representations of populations with a stable age structure, they have limitations in respect to density-dependent responses (e.g. density-dependent natural mortality) and dynamic processes (e.g. fishing and variable recruitment) that can be included in dynamic models. The latter types of

Table 1

Methods used to estimate mortality for *Rhizoprionodon taylori* from life history parameter relationships. *GSI* = gonadosomatic index; K = von Bertalanffy growth parameter; L_∞ = von Bertalanffy growth parameter; M = natural mortality; T = average water temperature; t_{max} = maximum age; x_m = age at maturity; Z = total mortality.

Method	Relationships
Hoenig (1983)	$\ln(Z) = 1.46 - 1.01 \ln(t_{max})$
Pauly (1980)	$\ln(M) = -0.0066 - 0.279 \log(L_\infty) + 0.6543 \log(K) + 0.4634 \log(T)$
Gunderson (1980)	$M = 4.64\,GSI - 0.370$
Gunderson and Dygert (1988)	$M = 0.03 + 1.68\,GSI$
Jensen (1996) (age)	$M = \frac{1.65}{x_m}$
Jensen (1996) (growth)	$M = 1.5K$ (theoretical)
Jensen (1996) (Pauly)	$M = 1.6K$

models require abundance data (e.g. CPUE time-series data or fishery-independent surveys) that are not available for many elasmobranch populations. In cases where abundance data are not available, demographic models may represent the best available technique for the analysis of stock dynamics.

The Australian sharpnose shark, *Rhizoprionodon taylori*, is an ideal example of a small, short-lived, fast growing, early maturing tropical species (Simpfendorfer, 1992, 1993). It is endemic in the inner continental shelf waters of northern Australia between the Northwest Shelf and southern Queensland (Last and Stevens, 1994). It is captured throughout much of its range as bycatch in commercial fishing operations, including gillnet fisheries for barramundi, mackerel, and shark, and prawn trawl fisheries (Simpfendorfer and Milward, 1993; Last and Stevens, 1994). This paper reports the results of mortality estimation and demographic analysis for *R. taylori*. Mortality was estimated in two ways. First, a number of relations between mortality and life history parameters from the literature were used to evaluate the appropriateness of these methods for estimating natural mortality in sharks. Second, catch curve analysis was conducted to produce a direct estimate of mortality. The results of the demographic analyses are used to comment on the probable sustainability of short-lived, fast growing, early maturing, tropical elasmobranch populations.

Materials and methods

Estimation of mortality

Two approaches were taken to estimate mortality in *R. taylori*. The first was to employ relationships between life history parameters and natural mortality (M) or total mortality (Z) from the literature. Seven relationships were chosen (Table 1) to investigate variability in their results. All seven were based heavily on data from teleost fish, although most included some data from elasmobranchs. The most widely used relationship in elasmobranch studies is that of Hoenig (1983), which uses a linear function to estimate total mortality from maximum age. Although this method estimates total mortality, it was assumed to represent natural mortality for *R. taylori* because there was little or no fishing for this species in the study area (Simpfendorfer, unpubl. data). The method of Pauly (1980) uses two parameters of the von Bertalanffy growth curve (L_∞ and K) and average temperature to estimate natural mortality. Jensen (1996) reanalyzed Pauly's (1980) data and found that natural mortality could be estimated with the same level of accuracy based only on the value of K. In the same paper Jensen (1996) also gave two other relationships for estimating natural mortality based on life history theory, one based on K and the other on age at maturity. The final two relationships selected used maximum female gonadosomatic index (GSI) as an indicator of reproductive effort to estimate natural mortality. The method of Gunderson (1980) was based on only 10 species; Gunderson and Dygert (1988) expanded this to 20 species. Data for calculation of M were taken from Simpfendorfer (1992; GSI) and Simpfendorfer (1993; von Bertalanffy parameters, maximum age, and age at maturity).

The second approach to the estimation of mortality was catch curve analysis (e.g. Ricker, 1975; Vetter, 1987). Age data for the catch curves were taken from Simpfendorfer (1993). Ages were converted to whole years and the natural log of the number of individuals ($\ln N$) was plotted against age for males and females

separately. Mortality for each sex was calculated as the negative value of the slope of the regression line for points to the right of, and including, the peak ln N value. Ricker (1975) used only points to the right of the peak ln N value to calculate mortality; however, the small number of age classes in *R. taylori* meant that including the peak value would increase the reliability of the estimate. To confirm that the peak ln N value should be included in the regression calculations, linear and quadratic functions were fitted to the data. If the quadratic function provided a significantly improved fit as judged by an F test, then it was assumed that the inclusion of the peak ln N value introduced significant curvature into the data set and so violated the assumption of catch curve calculations that mortality is constant across all age classes. In this situation the peak ln N value was not used in the calculation. As with the Hoenig (1983) method, the estimate of mortality from the catch curves was taken to be natural mortality because there was little or no fishing pressure on the stock from which the age data were collected.

Demographic analysis

Demographic analysis of *Rhizoprionodon taylori* was undertaken with standard life history table methods (e.g. Krebs, 1985). The parameters estimated from the life history table were net reproductive rate (R_0), generation time (G), intrinsic rate of population increase (r), and population doubling time (t_{X2}). Positive values of r indicate that a population is able to replace itself and thus will not decline, whereas negative values of r indicate that the population is unable to replace itself and will decline. Values of r were calculated by solving the Euler equation (Krebs 1985):

$$\sum_{x=0}^{x_{max}} l_x m_x \cdot e^{-rx} = 1$$

where x = age;
x_{max} = maximum age;
l_x = the proportion of animals surviving to the beginning of a given age class; and
m_x = age-specific natality.

Age and growth data for the demographic analysis were taken from Simpfendorfer (1993). Maximum age was taken as 6 years for males and 7 years for females, and age at maturity for males and females was taken to be one year. Because Simpfendorfer (1993) was not able to validate age estimates (but did have supporting marginal increment and length-frequency data), sensitivity tests were run to investigate the influence of the uncertainty of age estimates (maximum age 10 years, age at maturity 2 years).

Reproductive data were taken from Simpfendorfer (1992). Litter size varied significantly with maternal length (Fig. 1; r^2=0.33, P<0.05). Because observations of litter size were made throughout the year, the litter size for each age class was calculated from the size of females at the midpoint of the age class. Mature females produce a litter each year. The sex ratio of the embryos was not significantly different from 1:1; therefore the litter size for each age class was halved to give the number of female pups per female. Although *R. taylori* matures at the age of one, the first litter is not produced until the end of the second year. Thus only females that survive to the end of that age class produce young. To accommodate this in the life history table, age-specific natality was calculated from the number of animals surviving to the end of a given age class (i.e. the number at the start of the next age class). Similarly, the age-specific natality of the final age class was set to zero because it was assumed that no animals survived to the end of the last age class. To assess the difference in results between calculating age-specific natality from the number present at the beginning and end of an age class, separate life history tables were constructed and the results compared.

A life history table was constructed for each of the values for natural mortality, calculated as described above, to investigate the sensitivity of demographic parameters to different values. To simulate increased mortality of the youngest age class, a number of other authors have doubled the normal value of M for the first age class (e.g. Hoenig and Gruber, 1990; Smith and Abramson, 1990; Cailliet, 1992; Sminkey and Musick, 1996). A life history table was constructed with double the normal value of M for the first *R. taylori* age class to test the sensitivity of outcomes to this approach.

Fishing mortality (F) was incorporated into the survivorship function of the life history table such that total mortality was the sum of M and F. The critical value of F, at which r equaled zero (i.e. the level of fishing beyond which the population could not replace itself, F_c), was calculated for each life table. For the calculation of F_c, fishing mortality was assumed to be equal for each age class. Negative values of F_c occurred when the population was declining without fishing and indicated that the population could sustain no fishing. The main source of fishing mortality on *R. taylori* in northern Australia is gill nets, which do not normally catch animals until they are at least one year of age. To investigate the effect of the age at which F begins (age at first cap-

Table 2

Life history table for *Rhizoprionodon taylori* based on various estimates of female natural mortality (M). R_0 = net reproducdtive rate; G = generation time; r = intrinsic rate of population increase; t_{x2} = population doubling time; F_c = level of fishing beyond which the population can not replace itself.

Scenario	Source of M	M	R_0	G	r	t_{x2}	F_c
A	Hoenig (1983)	0.60	1.547	2.233	0.212	3.273	0.140
B	Pauly (1980)	1.34	0.200	1.442	–0.869	–0.798	–0.600
C	Jensen (1996) (age)	1.65	0.096	1.301	–1.297	–0.534	–0.910
D	Jensen (1996) (growth)	1.52	0.130	1.353	–1.119	–0.619	–0.780
E	Jensen (1996) (Pauly)	1.62	0.103	1.312	–1.256	–0.552	–0.880
F	Gunderson (1980)	1.49	0.140	1.366	–1.078	–0.643	–0.750
G	Gunderson and Dygert (1988)	0.70	1.123	2.063	0.057	12.102	0.038
H	Catch curve (female)	0.56	1.758	2.304	0.271	2.554	0.179

ture, AAFC) the values of r at different levels of F and AAFC were calculated. F after AAFC was assumed to be constant across all ages.

Results

Mortality

The calculation of M from the various life history relations produced estimates ranging from 0.6 to 1.65 (Table 2). All the methods based on von Bertalanffy growth parameters gave results greater than one. Only the Hoenig (1983) and Gunderson and Dygert (1988) methods yielded estimates less than 1.

The length and age frequency data for *R. taylori* on which the age analysis of Simpfendorfer (1993) was based are shown in Figure 2. Estimates of M from the catch curves were 0.698 for males and 0.561 for females (Fig. 3). The first age class (0) for both males and females was excluded from the regression analysis to estimate M because it was lower than, and to the left of, the peak ln N value. Fitting of quadratic functions to the data did not significantly improve the fit to the data points selected (male: F=3.86, P=0.188; female: F=1.35, P=0.329), confirming that their inclusion did not violate the assumption relating to constant mortality.

Demographic analysis

Life history tables were constructed to obtain demographic results for the eight different estimates of M for an unfished *Rhizoprionodon taylori* population (Table 2). Three of the eight (A, G, and H) gave positive values of r: the methods of Hoenig (1983), Gunderson and Dygert (1988) and the catch curve method. The catch curve and Hoenig (1983) methods produced similar demographic results, with r values between 0.2 and 0.3, and with doubling times of 2.5 to 3.5 years (Table 2). These were considerably higher than for the Gunderson and Dygert (1988) method, which gave an r value of 0.057 and a doubling time of 12.1 years. The values of r for the remaining scenarios (B–F) were all much less than zero (–0.869 to –1.297; Table 2), indicating population decrease even with no fishing.

The value of M from the catch curve method was used to test the sensitivity of the life history table values to changes in model structure and age parameters. There was a large difference in age-specific reproductive rate calculated with a proportion of the

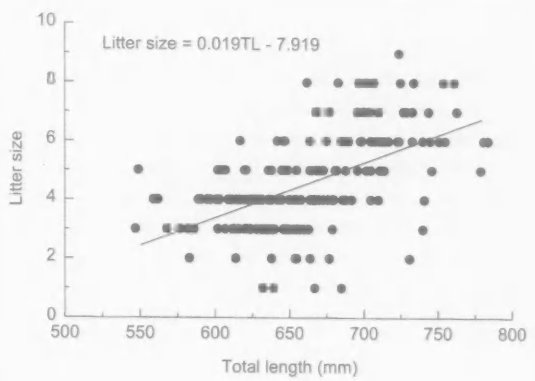

Figure 1

Litter size of *Rhizoprionodon taylori* as a function of maternal length. Data from Simpfendorfer (1993).

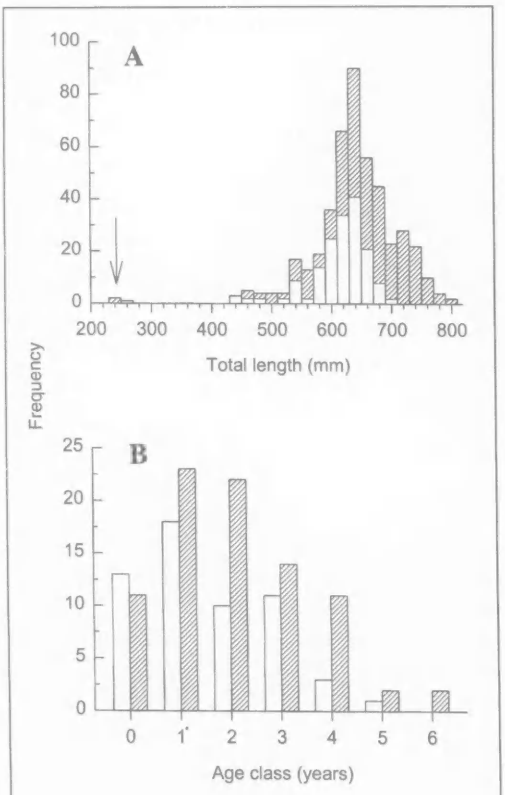

Figure 2

(A) Length and **(B)** age-frequency distributions of male (open bars) and female (hatched bars) *Rhizoprionodon taylori* from the waters of Townsville, Queensland. The arrow indicates size at birth.

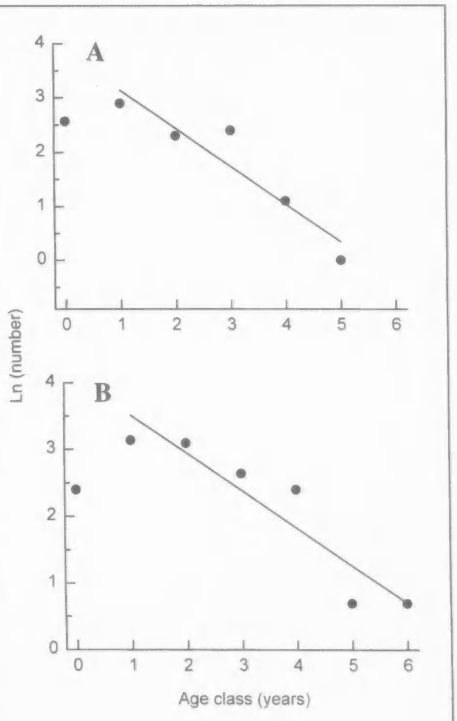

Figure 3

Catch curves for **(A)** male and **(B)** female *Rhizoprionodon taylori* derived from data from Simpfendorfer (1993). Data points for the first age class were not used to calculate regression lines.

population surviving to the beginning of an age class (J) rather than to the end (I). The value of r increased from 0.271 to 0.600, doubling time decreased from 2.544 years to 1.155 years, and the maximum value of F sustainable by the population (F_c) increased from 0.179 to 0.600 (Table 3) when the beginning of an age class was used. Doubling the value of M in the first year of life (I vs. K) caused a reduction in the value of r from 0.271 to 0.001, and population doubling time increased from 2.544 to 529.2 years (Table 3). The maximum level of fishing mortality that the population could sustain under such a scenario decreased from 0.179 to 0.001. Doubling first-year M and also calculating age-specific natality from the number surviving at the beginning of age classes (L) produced results identical to the base case (Table 3).

Increasing the maximum age to 10 years resulted in a small increase in r, from 0.271 to 0.276, and decreased population doubling time from 2.544 to 2.516 years (Table 3). Setting age at maturity at two years instead of one resulted in an r of 0.035, and a population doubling time of 19.82 years (Table 3).

Values of r varied considerably with changes in F and AAFC (Fig. 4). With an AAFC of 0, F_c = 0.18; with an AAFC of one, F_c = 0.27; and with an AAFC of two, F_c = 0.67. When AAFC was three or more the population was sustainable at F values up to at least 1.0.

Discussion

Mortality estimates

In most studies where natural mortality has been estimated for shark populations, particularly for use in demographic analysis, indirect estimation methods have been used (e.g. Hoenig and Gruber, 1990; Cortes, 1995; Sminkey and Musick, 1996; Au and Smith, 1997). The results of the current study indicate that these indirect methods may provide a wide

Table 3

Sensitivity of life history tables to changes in model structure and age parameters. $l_{x+1}m_x$ indicates that age-specific natality was calculated from the number sharks surviving to the end of age classes; l_xm_x indicates that age-specific natality was calculated from the numbers surviving at the beginning of classes; $2M_1$ indicates that natural mortality was doubled for the first age class; $1M_1$ indicates that natural mortality was constant for all age classes. Definitions of parameters are given in Table 2.

Scenario	Sensitivity test	R_0	G	r	t_{x2} (years)	F_c
I	Base case ($l_{x+1}\,m_x$, $1M_1$)	1.758	2.304	0.271	2.554	0.179
J	$l_x\,m_x$, $1M_1$	3.080	2.304	0.600	1.155	0.600
K	$l_{x+1}\,m_x$, $2M_1$	1.003	2.304	0.001	529.2	0.001
L	$l_x\,m_x$, $2M_1$	1.758	2.304	0.271	2.554	0.271
M	Maximum age = 10	1.820	2.488	0.276	2.516	0.183
N	Age at maturity = 2	0.035	3.061	0.035	19.82	0.026

range of estimates of natural mortality for a single population. Testing these values of natural mortality for *R. taylori* in life history tables showed that most of the methods produce values of r that would result in a population decreasing even when it was unfished. Such a result is biologically unreasonable. In contrast, Simpfendorfer (1999) made similar comparisons of indirect estimation methods for the dusky shark (*Carcharhinus obscurus*) and found that results did not differ greatly between methods. The difficulties in applying many of the indirect methods to *R. taylori* may relate to its short lifespan and fast growth because all but two of the methods used age or growth parameters to estimate natural mortality.

Among the indirect methods for estimating natural mortality, only those of Hoenig (1983) and Gunderson and Dygert (1988) yielded estimates that would allow an unfished population to increase. Although the values of natural mortality from the two methods were relatively similar (0.60 and 0.70, respectively), they produced different results when used in the life history tables to calculate r, with the Hoenig (1983) estimate producing a much higher value. This difference indicates that the results of demographic analysis are highly sensitive to changes in natural mortality. It is unlikely that the Gunderson and Dygert (1988) method produced a realistic value of natural mortality because it is based on the assumption that GSI is an index of total reproductive effort. Although this is true for most fish species, it is not the case for placental forms (such as *R. taylori*) in which much of the energy invested in reproduction is supplied during development rather than stored in the ovary prior to fertilization. Of the indirect methods used, the Hoenig (1983) method is therefore likely to be the most realistic estimate of natural mortality for *R. taylori*.

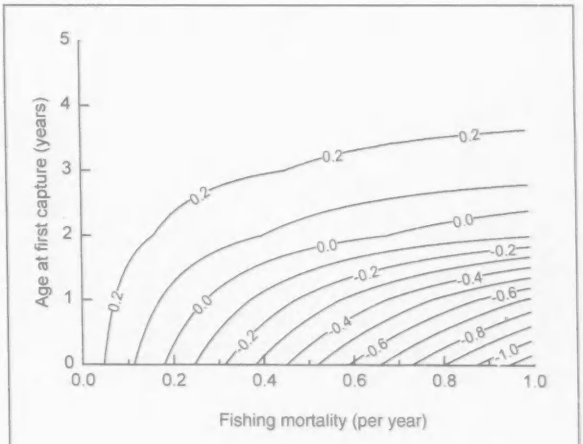

Figure 4

Contour plot of intrinsic rate of population increase (r) as a function of fishing mortality (F) and age at first capture (AAFC) for *Rhizoprionodon taylori* from northern Australia. Estimates are based on a life table where natural mortality was calculated by a catch curve (scenario H in Table 2). Fishing is sustainable at values of $r > 0$.

There are relatively few studies of shark populations in which natural mortality has been estimated directly with either tagging studies (e.g. Grant et al., 1979; Manire and Gruber, 1993) or catch curves (e.g. Cortes and Parsons, 1996). Although direct approaches to determining mortality would be expected to produce more realistic estimates, they must also meet a number of criteria in order to produce accurate results. The assumptions for the catch curve technique used in the present paper included constant mortality, recruitment, and selectivity over all age classes used in the calculations as well as random collection of samples from the population. The

data on which the calculations for *R. taylori* were based are likely to have met at least two of these assumptions. Because the area from which samples were collected was subject to little or no fishing, the population size should have remained relatively constant and thus fluctuations in recruitment would be minimized. The necessity of excluding the first age class from the catch curve analysis resulted from the selectivity of the gill nets used to collect specimens. For the age classes included in the analysis, the size of individuals was similar because growth rapidly reaches an asymptote, and therefore selectivity was probably reasonably constant. The assumption that mortality was constant was more difficult to test. However, the small size of *R. taylori* and the small change in its size after the first year or two of growth (Simpfendorfer, 1993) suggest that all age classes are likely to be subject to similar levels of predation.

The estimates of natural mortality for female *R. taylori* from the catch curve and from the indirect method of Hoenig (1983) were similar: 0.56 and 0.60, respectively. Such a finding is contrary to that reported by Cortes and Parsons (1996), who suggested that the Hoenig (1983) method would produce lower natural mortality estimates than those from catch curves. The present study suggests that for some species the Hoenig method will produce acceptable results. However, Cortes and Parsons' (1996) caution that demographic studies based solely on a natural mortality estimate from the Hoenig (1983) method should still be heeded because it is clear that the accuracy of this method may vary between species.

The most biologically plausible estimates of natural mortality for *R. taylori* (0.698 for males and 0.561 for females) are significantly higher than those reported so far for many other species of shark. Species with mortality levels of a similar magnitude are the bonnethead shark (*Sphyrna tiburo*) (0.625; Cortes and Parsons, 1996) and the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) (0.42; Cortes, 1995). Each of these three species (*R. taylori, R. terraenovae,* and *S. tiburo*) are short-lived (6–12 yr). In longer-lived shark species, estimates of natural mortality are much lower. For example, Sminkey and Musick (1996) estimated an M of 0.105 for *Carcharhinus plumbeus*, which lives at least 30 years, and Smith and Abramson (1990), Cailliet (1992), and Au and Smith (1997) estimated that *Triakis semifasciata*, which lives to 30 years, has an M between 0.139 and 0.15.

The small size of *R. taylori* probably results in it being subject to high levels of predation throughout life. The small size at birth (220–260 mm) means that the first age class is particularly vulnerable to predation. The results of the sensitivity test, in which natural mortality was doubled for the youngest age class, indicate that this technique, which has previously been used to account for increased predation of young sharks, was not realistic for *R. taylori*. This is a result of the high value of natural mortality assumed for older age classes. It was not possible to estimate what, if any, increase in predation occurs for the youngest age class of *R . taylori*. However, any increase in predation would result in reduced estimates of r.

Demographic analysis

The most likely demographic results for *R. taylori*, those based on natural mortality estimated from the catch curve, indicate that the maximum value of r is about 0.27. This value is one of the highest for a species of shark. Cortes and Parsons (1996) estimated a similar rate (0.272–0.283) for *Sphyrna tiburo* from Florida with Hoenig's method to estimate natural mortality. *Rhizoprionodon taylori* and *S. tiburo* have similar life histories, with short lifespans, rapid growth, early maturity, and high natural mortality. All other published studies of shark demography have estimated intrinsic rate of increase at less than 0.1 (e.g. Hoenig and Gruber, 1990; Cailliet, 1992; Cailliet et al., 1992; Cortes, 1995; Sminkey and Musick, 1996; Au and Smith, 1997; Cortes, 1998). In most cases these species have been longer lived and slower to mature and have exhibited lower natural mortality than *R. taylori* or *S. tiburo*. The exception to this is *R. terraenovae*, which grows larger than *R. taylori* and is relatively short-lived (10 yr), but has a lower reproductive rate (Cortes, 1995).

Demographic analysis of *R. taylori* is sensitive to the way age-specific reproductive rate is calculated because of this species's short lifespan. Whether age-specific natality is calculated on the basis of the proportion of a population surviving at the beginning or the end of an age class leads to a very large difference in r. This effect is magnified by the high natural mortality of *R. taylori*. It is therefore important to take account of gestation period in the calculation of reproductive rate. This is less important in longer lived species in which natural mortality is lower and in which there is a relatively small difference between the proportions of a population surviving until the beginning and the end of an age class.

This study indicates that accurate age data are required for demographic analysis. The results for *R. taylori* showed a high level of sensitivity to changes in age at maturity, but only limited sensitivity to changes in maximum age. Given that the age data on which this research were based have not been validated, there remains some uncertainty about the results. Further work to validate these data (espe-

cially age at maturity) would decrease uncertainty. However, the length-frequency data supplied by Simpfendorfer (1993) support the hypothesis that *R. taylori* mature at age one and produce their first litter at age two.

Increasing age at first capture for *R. taylori* increased the level of fishing mortality that the population could sustain. Allowing individuals to remain unfished until they had produced one litter (AAFC=2) made fishing mortality levels up to 0.67 sustainable, whereas any level of fishing mortality was sustainable if individuals were allowed to produce two litters (AAFC=3). In a practical sense, AAFC restrictions are implemented as size restrictions. On the basis of the growth curves given by Simpfendorfer (1993), size of female *R. taylori* at the end of each of the first three years is 55, 67, and 71 cm total length (TL), respectively. The fact that size changes only slightly after the first two years makes the use of age restrictions unworkable for older individuals.

The gillnet fishery in which *R. taylori* is most often captured in northern Australian waters uses mesh sizes no smaller than 10 cm (stretched mesh). Gill nets of this size rarely catch animals less than 60 cm TL. The age at first capture in this fishery is therefore approximately one year. Although *R. taylori* less than one year of age are caught by trawlers, this fact was noted by the author only once in observations of research trawls between 1986 and 1992 in the Townsville region. On the basis that age at first capture of *R. taylori* in northern Australia is probably one year, demographic analysis indicates that the level of fishing mortality (F_c) that the population can sustain is approximately 0.27. However, Ricker (1975) showed that the level of fishing mortality needed to achieve maximum sustainable yield (MSY) is $r/2$. Thus for *R. taylori* $F_{MSY} = 0.135$.

Sustainability of fisheries

The comparison of demographic assessments of short-lived, fast growing, early maturing elasmobranch species such as *R. taylori* and *S. tiburo*, to those of longer-lived, slow growing, late maturing species indicates that they are likely to be able to sustain higher levels of fishing pressure than the latter species. For example, Sminkey and Musick (1996) reported that *Carcharhinus plumbeus* was most likely to be sustainable when $F_c \leq 0.1$, or $F_c = 0.25$ if a minimum size of 178 cm was used. Similarly, Cailliet (1992) reported that for *Triakis semifasciata*, $F_c = 0.084$ did not reduce the population, but that fishing mortality at double this level was sustainable only if animals 12 years and older were caught. This contrasts markedly with the results for *R. taylori* that the population may be sustainable at F_c=0.18, or F_c = 0.27 if age at first capture was one year. It is therefore possible that at least some species of elasmobranchs, in particular the shorter-lived, fast growing, early maturing species, are able to sustain limited commercial levels of fishing pressure. The apprehensive conclusion of Holden (1974) regarding sustainable fishing of elasmobranch stocks may need to be revised for selected species. However, the real challenge is to manage the development and regulation of such elasmobranch fisheries effectively.

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Reproduction and feeding of spotted gully shark, *Triakis megalopterus*, off the Eastern Cape, South Africa

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Abstract.—The spotted gully shark, *Triakis megalopterus*, was sampled opportunistically over a 12-year period from catches of shore and ski-boat fishermen using hooks and lines. Most specimens (89.6%) were taken from rocky reefs less than 10 m deep, 8% were caught at 11–20 m, and only 2.4% were recorded from waters more than 20 m deep. The reproductive biology of 35 males and 87 females was examined. The spotted gully shark exhibits aplacental viviparity. Size at 50% maturity for males is ca. 1320 mm total length (TL) and for females ca. 1450 mm TL. Maximum sizes recorded here were 1520 mm TL for males and 2075 mm TL for females. Gestation appears to last 19–21 months. The female reproductive cycle may be 2–3 years, depending on the time between pregnancies. The sex ratio of embryos was found to be 1:1 but the postpartum male:female ratio was 1:2.5. Size at birth was estimated to be 420–450 mm TL. The smallest free-swimming individual recorded was 576 mm TL. Number of embryos per pregnancy ranged between 5 and 15, with a mean of 9.7. A total of 110 stomachs were examined in the feeding study. Diet changed with increase in shark size. Small sharks (<1 m) preyed mainly on Cape rock crabs, *Plagusia chabrus* (78% of mass), whereas sharks of 1–1.4 m preyed largely on Cape rock crabs (48%) and cephalopods (33%). Teleosts were more important for sharks larger than 1.4 m (54%); most of these prey were associated with rocky reefs.

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The genus *Triakis* Müller and Henle, 1838, commonly called leopard shark, comprises small to moderately large, harmless, stocky sharks that feed on invertebrates and fish. *Triakis* is currently restricted to five species: *Triakis acutipinna* Kato, 1968 (sharpfin houndshark); *T. maculata* Kner and Steindachner, 1867 (spotted houndshark); *T. scyllium* Müller and Henle, 1839 (banded houndshark); *T. semifasciata* Girard, 1854 (leopard shark); and *T. megalopterus* (Smith, 1849) (sharptooth houndshark or spotted gully shark; Compagno, 1988).

Triakis megalopterus is a stout houndshark with a broadly rounded snout and a large mouth with small, pointed teeth. The head and body are gray or bronze above, usually with numerous small black spots, and white underneath (Bass et al., 1975). It is endemic to southern Africa (Compagno et al., 1989), where it occurs from northern Namibia, at about 21°45'S, 13°57'E, to Coffee Bay in Eastern Cape, South Africa, at 31°59'S, 29°09'E. The species is a common inshore bottom-dwelling shark of temperate continental waters, where it is caught by anglers in shallow subtidal waters. It prefers rocks and crevices in the shallows and is confined to water shallower than 50 m along the Cape coast (Bass et al., 1975; Compagno et al., 1989, 1991).

Very little has been published on the biology of this species (Bass et al., 1975). Although all five species of *Triakis* are viviparous, they lack yolksac placentas and the embryos obtain nourishment from their yolk sacs (Bass et al., 1975; Castro, 1983; Compagno, 1984; Kusher et al., 1992). Bass et al. (1975) and Compagno (1984) provided some information on the food habits of *T. megalopterus*, noting the presence of crabs (*Plagusia chabrus*), teleost fishes, and one small shark (*Scyliorhinus capensis*) in stomach contents.

At present, there is no scientific information that could guide management decisions on *T. megalopterus*, with the possibility of a small population size and limited range distribution (Compagno et al. 1989; Goosen, 1997), this species could be vulnerable to overexploitation in inshore multispecies shark fisheries. Off California, *T. semifasciata* has declined in abundance and consequently management measures have been proposed there (Smith and Abramson, 1990; Cailliet, 1992).

The aim of this study was to investigate the reproductive and feeding biology of *T. megalopterus*. Investigations of age and growth will be documented elsewhere. Improved knowledge of this species could underpin management strategies for this component of the multispecies shark fisheries off South Africa, which are known to be expanding (Smale, 1997).

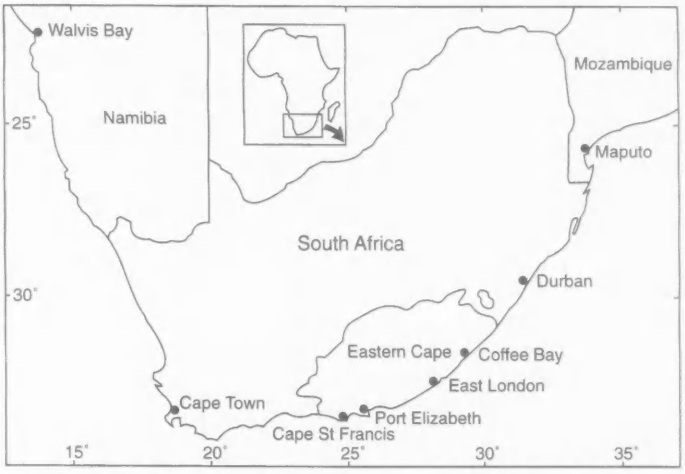

Figure 1
Southern Africa showing places mentioned in the text.

Materials and methods

Specimens were collected over a 12-year period, between February 1984 and October 1996, from catches made with hooks and lines by rock, surf, and skiboat fishermen. All specimens used in this study were collected along the Eastern Cape coastline between Cape St. Francis (34°12'S; 24°52'E) and Coffee Bay (31°59'S; 29°09'E), South Africa (Fig. 1). Specimens collected for biological sampling were examined as soon as possible after capture, or were frozen for later study. Sharks were measured to the nearest millimeter and, where possible, weighed with a spring scale accurate to 100 g. Measurements of total length (TL) can vary considerably depending on the placement of the caudal fin during measurement (Branstetter et al., 1987); in this study TL was measured on a horizontal line between perpendiculars, from the tip of the nose to the tip of the tail, with the tail at its maximum extension (Compagno, 1984). Total length is used throughout this paper, unless otherwise noted.

Reproductive information was collected for 35 males and 87 females. Maturity stages largely followed Bass et al. (1975), with minor modifications (Goosen, 1997). Each specimen was assigned to one of the reproductive stages: embryo, immature, adolescent, mature, and, in females, pregnant. The clasper was measured in length from the point of outside insertion in the pelvic fin to the tip of the clasper (CLO); from the point of insertion at the cloaca to the tip of the clasper (CLI); and in width at its thickest point (CBW) (Compagno, 1984). For females, the following data were collected: diameter of the two largest ovarian eggs, width of the oviducal gland, greatest width of the uterus, absence or presence of embryos and uterine eggs, and numbers of embryos and eggs if present.

Embryos were measured, sexed, and weighed. The mean length of embryos in each litter was calculated after abnormally developed individuals were excluded. Seasonality of mating, gestation period, and pupping season were examined by comparing embryo sizes in different months. Hepatosomatic indices (HSI) were calculated from the formula

$$HSI = (LW/BW) \times 100,$$

where LW = liver weight in grams; and
BW = total body weight in grams.

Stomach contents were examined as soon as possible after capture, or frozen for later analysis. Prey were identified to the lowest possible taxon. Excess liquid was drained off and the mass of the remains determined to the nearest 0.1 g on a top-loading pan balance. Bait used to capture the sharks was excluded from analyses.

Size measurements used for prey were carapace width (CW) in crabs, mantle length (ML) in cephalopods, and total length (TL) in teleosts and all other prey. After whole fish prey were measured, otoliths were removed to verify identification and paired, counted, and measured. Otoliths were used to identify well-digested prey and to estimate their length. Similarly, cephalopod beaks were collected, counted, and measured. Neither formalin nor alcohol was used to store stomach contents, because otoliths exposed to such preservatives become etched or brittle (Smale et al., 1995). Lengths of well-digested cephalopods and teleosts were determined from regressions relating beak and otolith lengths to body length (Smale, 1983; Smale et al., 1993, 1995). Digested otoliths had a chalky eroded appearance and were not measured for use in prey size estimates.

Diet was quantified by 1) frequency of occurrence (%F), the ratio of stomachs containing a particular prey to stomachs containing any prey, expressed as a percentage; 2) numerical importance (%N), the number of each prey expressed as a percentage of the total number of prey items; and 3) gravimetric importance (%M), the wet mass of a prey category as a percentage of the total weight of the stomach contents (Hyslop, 1980). By using all three methods of analysis, we avoided bias associated with the use of any one method (Hynes, 1950; Windell, 1968; Hyslop, 1980). No combination of methods was used because this may have resulted in combining sources of error (Berg, 1979). Reconstituted prey weights were not used because bias may have been introduced as a result of the different digestion and accumulation rates of fish otoliths and cephalopod beaks (Smale, 1983). Consequently, the actual wet mass of each item in stomachs was used to investigate prey composition in this study (Smale, 1991).

Preliminary analyses revealed considerable differences in prey between sharks of different sizes, and samples were subsequently divided into three arbitrary size classes: less than ≤999 mm, 1000–1399 mm, and ≥1400 mm TL. To investigate the relation between sizes of predator and prey, reconstructed prey lengths and masses were calculated with otolith and beak measurements. Recorded wet masses and carapace widths and lengths had to be used for crustaceans, and only intact crustaceans were included in the predator–prey size analysis. Common names used for crustaceans are after Holthuis (1991).

Results

Depth range

Material collected in this study was derived from fishermen exploiting a wide range of depths. Both shore-based and boat-based catches were sampled, although the proportion of effort in different depth ranges was not quantifiable. Nevertheless, *T. megalopterus* was taken mainly from shallow water. Of 125 specimens where collection depth was known, 89.6% were taken in shallow waters of 10 m and less. Only 8% were collected at 11–20 m and 2.4% at >20 m. The greatest capture depth recorded in this study was approximately 30 m, at an offshore bank. No obvious size-based habitat segregation was evident in this relatively small sample.

Size range and maturation

The overall male-to-female ratio in sharks sampled was 1:2.5. The smallest male and female sharks captured were 576 mm and 725 mm, respectively. Females attain larger sizes than males; the largest male sampled was 1520 mm, compared with the largest female of 2075 mm. The clasper length (CLI) of the smallest male was 43 mm and that of the largest (a male of 1402 mm TL) was 239 mm (Fig. 2A). Based on clasper size, degree of calcification, and presence of sperm in the seminal vesicle, maturation in these sharks begins at about 1210 mm and is complete at about 1369 mm (Fig. 2A). Claspers of one specimen of 1345 mm were not quite rigid but sperm presence was noted. The smallest mature male was 1250 mm and the largest immature male was 1196 mm. The claspers of adults measured, on average, 225 mm (range 205–239 mm, n=16).

Increase in the diameter of ovarian eggs indicates the beginning of maturation. Small eggs (<4 mm diameter) could be seen in the ovaries of females of 977 mm and larger. Egg diameter increased noticeably in specimens larger than 1460 mm (Fig. 2B). Mature females had yellow yolk-filled ova larger than 4 mm in diameter. The developing uteri appear as thin strips of translucent tissue with diameters of up to 2.5 mm in females smaller than 1365 mm. As maturation proceeds, the uterus widens first at its posterior end, becoming bottle-shaped at lengths of 1391–1405 mm, with a diameter of 4–16 mm at its widest part (Fig. 2C). One female of 1490 mm TL had a uterus width of 16 mm. All females over 1460 mm, except the previously mentioned individual, had uterus widths wider than 20 mm, and all adult females had uterus widths measuring 20–140 mm ($\bar{x}$=82.81, n=27). The oviducal gland was difficult to distinguish in the smallest females but usually measured between 3 and 7 mm ($\bar{x}$=5.64, n=14) in females of less than 1365 mm, and grows little until females reach 1460 mm (Fig. 2D). All females over 1460 mm had oviducal glands wider than 20 mm and all adult females, both pregnant and non-pregnant (resting), had oviducal glands measuring 20–51 mm ($\bar{x}$=31.7, n=29). The smallest pregnant female measured 1465 mm TL.

Reproduction

Of 48 sexually mature females sampled, 81% were pregnant. The number of embryos per litter ranged from 5 to 15 ($\bar{x}$=9.7, n=38). One female had 16 egg cases, but of these only 13 had normal embryos, one was empty, and two contained retarded embryos (length 6.5% of the next smallest embryo length). Considering the size of the female (1650 mm TL), it is possible that litters of up to 16 pups may be recorded. There is no significant difference in the number of embryos between left and the right uteri

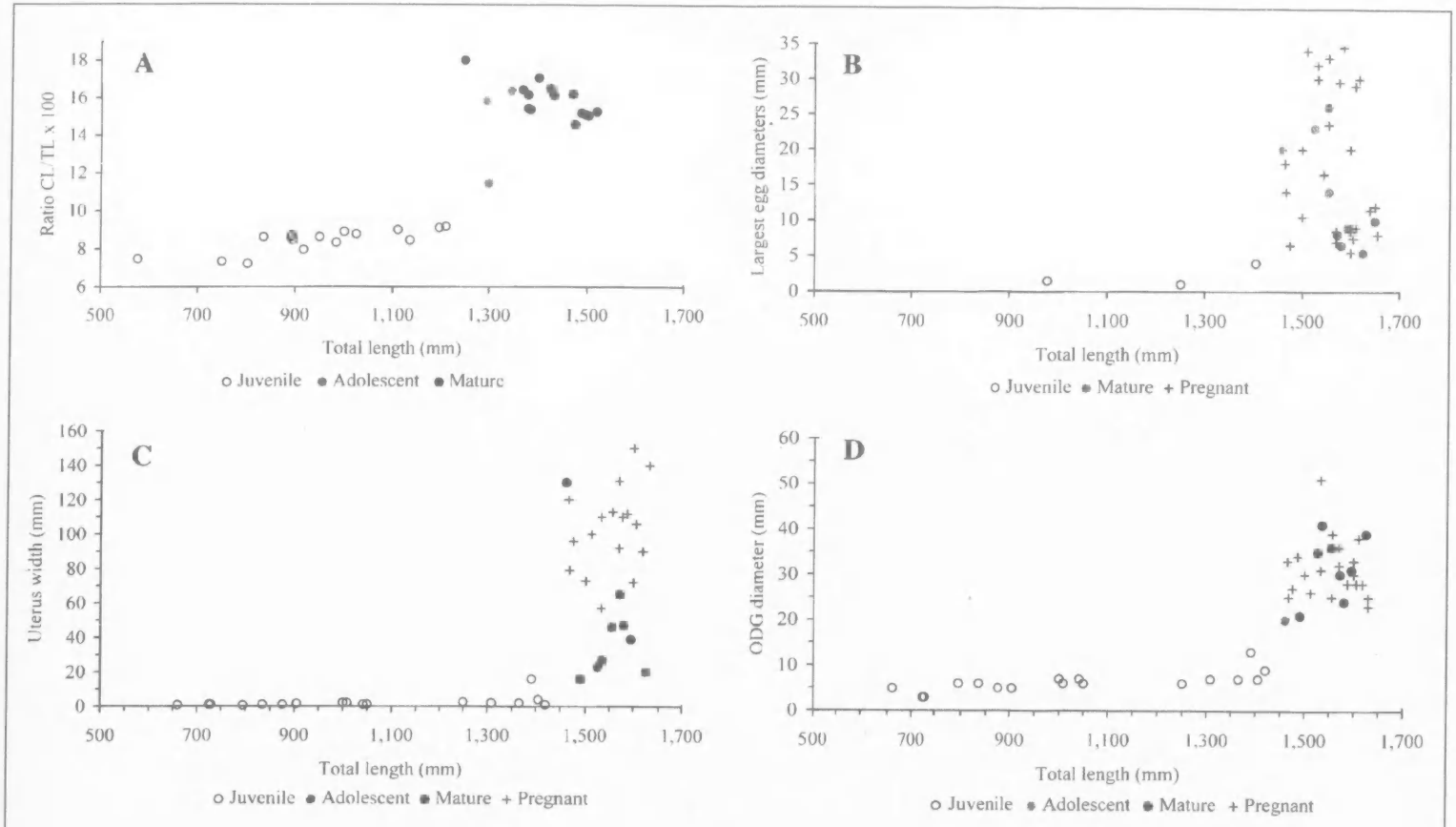

Figure 2

(A) Relation between inner clasper length (CLI) and total shark length, expressed as a percentage of total length. **(B)** Relation between diameter of the two largest ovarian eggs in each female and total length of female sharks. **(C)** Uterus width plotted against total length of female sharks. **(D)** Oviducal gland width plotted against total length of female sharks.

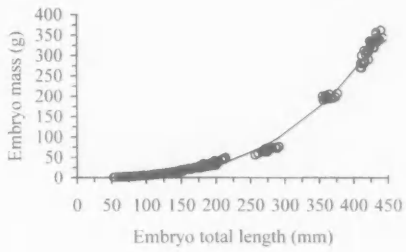

Figure 3

The relation between embryo mass (EM) and total embryo length (TL) was $EM = 2.397 \times 10^{-6} \times TL^{3.089}$ (r=0.99, n=275).

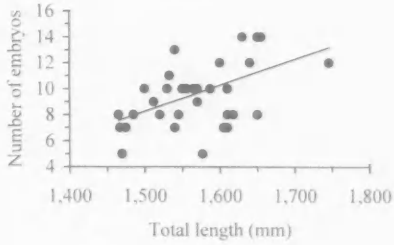

Figure 4

The relation between the number of normal embryos (n) and total length (TL) of pregnant females was $n = -21.74 + 0.020 \times TL$ (r=0.52, n=38).

(paired t test; P>0.5). Of the 244 embryos that were sexed, 122 were male and 122 were female.

The relation between wet body mass and total length of embryos was described by a power curve (Fig. 3):

$$W = 2.397 \times 10^{-6} \times TL^{3.089}, \qquad [r^2=0.994;\ n=275]$$

where W = embryo weight; and
TL = embryo total length.

Weight of near-term embryos ranged from 300 to 362 g ($\bar{x}$=331.4 g; n=23).

During all stages of development, the embryos within a uterus often differed in size; the largest embryos were as much as 30% longer than the smallest. Greater differences were found in early stages of embryonic development. Larger embryos usually occupy a more posterior position, suggesting that they are older than litter mates in more anterior positions. The embryos in both uteri were at equivalent developmental stages in all the samples. Embryo orientation within the uteri was normally head forward. Only two embryos from one batch lay head backward. Description of the developmental morphology of embryos was given by Goosen (1997).

Average observed embryo length in females between 19 May and 25 August was 425 mm (n=30). A female caught on 19 May had an embryo length range of 416–443 mm ($\bar{x}$=431 mm; n=15), whereas another female, caught on 25 August, had embryos in the length range of 412–440 mm ($\bar{x}$=425 mm; n=8). Yolk sacs were barely visible in the smaller of these embryos, and the largest had closed umbilical scars between the pectoral fins. Denticles and teeth of larger ones had erupted from the skin; one or two black spots were noted on some embryos. Their large size and eruption of teeth and denticles suggested that they had developed approximately to term. No embryo examined during this study showed any sign of a placental attachment between embryonic and maternal tissue. Embryos were readily removed from the uterus at all stages of development. Embryos are separated from each other in the uterus by enveloping uterine membranes, from which they apparently emerge shortly before birth. The largest embryo measured 443 mm and weighed 341 g. Based on available information, size at birth is estimated at 420–450 mm; birth probably occurs between May and August. The smallest free swimming individual, 576 mm in length, was taken in August.

Careful examination of embryos and uterine eggs showed that some of the uterine eggs failed to develop. Of 39 pregnant females, 11 (28%) had some nondeveloping uterine eggs. The greatest number of nondeveloping uterine eggs carried by a single female was 4 out of a total of 11, but most had only one or two. Of these pregnant females, 10 (26%) contained empty egg cases (no yolk). The largest number of empty egg cases carried by a single female was 12 (out of a total of 12). Occasionally, one embryo in a litter was deformed or retarded in growth. Because of the nondevelopment of a small proportion of uterine eggs, the number of developing, apparently normal embryos is a better measure of reproductive output than the number of uterine eggs. The relation between number of normal embryos and total length of the mother may be described by a linear regression (Fig. 4):

$$n = -21.74 + 0.02\ TL, \qquad [n = 38]$$

where n = litter size; and
TL = the total length of the mother in mm.

Litter size was found to be significantly correlated with total length of the mother ($P<0.01$, $r=0.52$, $n=38$).

The relation between shark length and liver mass was very variable but approximated a power relation (Fig. 5). The maximum recorded weight of females was about three times that of males; variation was higher in mature and pregnant individuals than in immature individuals.

To investigate the possible function of the liver as an energy source during pregnancy, female HSI was plotted against mean embryo TL (Fig. 6). Although the trend appeared negative, there was no significant correlation between mean embryo length and HSI ($r=0.242$, $P>0.05$; $n=31$).

Plotting mean embryo size against month of the year resulted in a scatterplot with two clusters of points but with no clear trend (Fig. 7). Extending the time axis to 24 months and shifting the larger embryos 12 months along the time axis yielded a clear trend. This finding would suggest that there is a gestation period of 19–21 mo and that the entire cycle spans approximately two years, excluding any resting period. Of a subsample of 11 mature females taken between May and August, four (36%) were resting (they showed no sign of recent pregnancy and had only small ova in the ovary) and the rest were pregnant, five (46%) with pups of intermediate size and two (18%) with large, near-term pups.

Feeding

A total of 110 stomachs were examined, consisting of 34 males (576–1520 mm TL) and 76 females (660–1746 mm TL). Females had a higher percentage of empty stomachs (20.5%) than males (12.1%). Preliminary analysis indicated a change in diet with predator size. This was investigated by grouping the data into three arbitrary size classes: smaller than ≥999 mm TL, 1000–1399 mm TL, and ≥1400 mm TL and longer. Prey taken clearly changes with increasing size (Fig. 8). Although invertebrates were important initially, larger sharks took more vertebrates (Table 1).

Small sharks fed almost entirely on crabs (Fig. 8). The Cape rock crab, *Plagusia chabrus*, dominated in the smaller two size classes of shark, in terms of mass (78.3% and 48.5%, respectively; Table 1). Larger crustacean taxa appeared in the diet of larger sharks. Cape slipper lobster, *Scyllarides elisabethae*, appeared in the second size class and Cape rock lobster, *Jasus lalandii*, and scalloped spiny lobster, *Pan-*

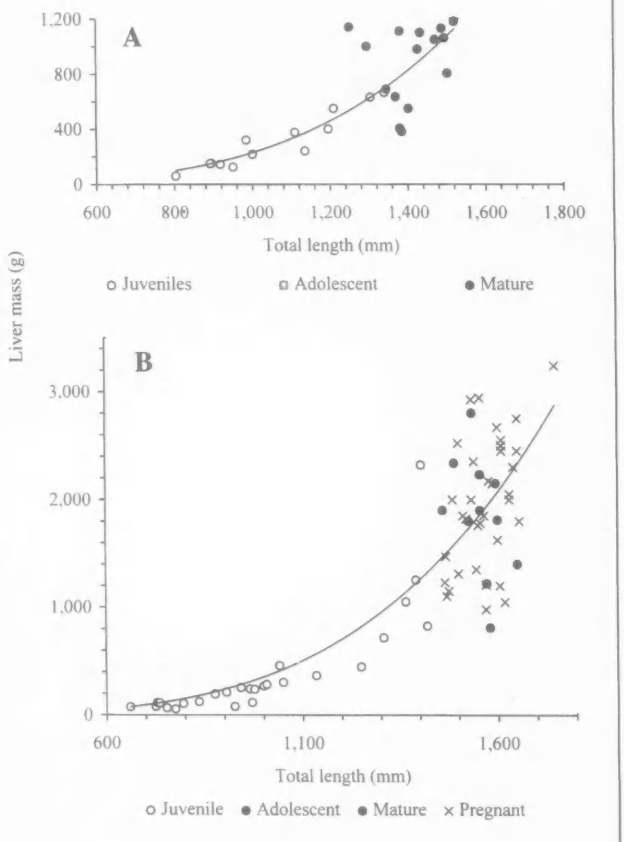

Figure 5

(A) The relation between liver mass (LM) and total length of male *T. megalopterus* was $LM = 9.517 \times 10^{-10} \times TL^{3.794}$ ($r=0.83$, $n=28$). **(B)** The relation between liver mass (LM) and total length of female *T. megalopterus* was $LM = 1.964 \times 10^{-9} \times TL^{3.752}$ ($r=0.86$, $n=73$).

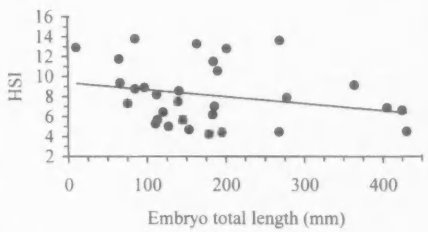

Figure 6

The relation between hepatosomatic index (HSI) of pregnant females and the mean length (TL) of normally formed embryos in the litter was $HSI = 9.376 - 0.0068\ TL$ ($r=0.242$, $n=31$).

ulirus homarus, appeared in the largest size class. Although crustaceans were important prey of the large sharks, they were less dominant in the diet.

Teleosts became more important prey for larger sharks. They included representatives from at least 10 families and 14 species (Table 1). They dominated the prey of large sharks by mass (53.9%) and by number (47%), whereas they contributed only 10.3% and 14.2% by mass for the medium and small-size classes, respectively (Fig. 8). Only three species of fish were eaten by the smallest sharks, of which barred fingerfin, *Cheilodactylus pixi*, was the most important. Six species were taken by the medium-size class, and twotone fingerfin (*Chirodactylus brachydactylus*) was the most important. The diet of the large-size class was dominated by several species, *viz.* seacatfish (*Galeichthys* sp.), cob (*Argyrosomus inodorus*), red tjortjor (*Pagellus bellottii natalensis*), and blue hottentot (*Pachymetopon aeneum*). The two largest teleost species ingested, based on recalculated total length, were a 336-mm sand steenbras (*Lithognathus mormyrus*) and a 334-mm seacatfish (*Galeichthys* sp.). Both were taken by sharks longer than 1500 mm TL.

Cephalopods were the second most important forage category for medium-size sharks (Fig. 8). The common octopus (*Octopus vulgaris*) and the squid *Loligo vulgaris reynaudii* were the most important species, making up 25.5% and 7.8% by mass, respectively. Cephalopods were minor prey for the largest class of sharks (4.6% by mass).

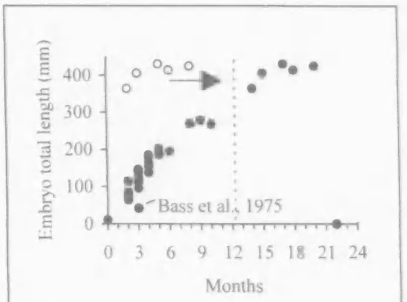

Figure 7

Mean size of normal embryos in each litter plotted against month of the year. The arrow indicates a shift of large litters (empty circles) to the same months one year later.

Elasmobranchs were relatively unimportant prey of spotted gully sharks. One stomach had the remains of a lesser sandshark (*Rhinobatos* sp.), another contained remains of a brown catshark (*Haploblepharus fuscus*), and two contained catshark eggs. The occurrence of anomalous food items was very rare. Inedible remains included a bryophyte (one stomach) and an unidentified mussel (one stomach).

In addition to ontogenetc variation in prey, prey size increased with growth (Fig. 9). Cape rock crab (*Plagusia chabrus*) was an important prey for sharks

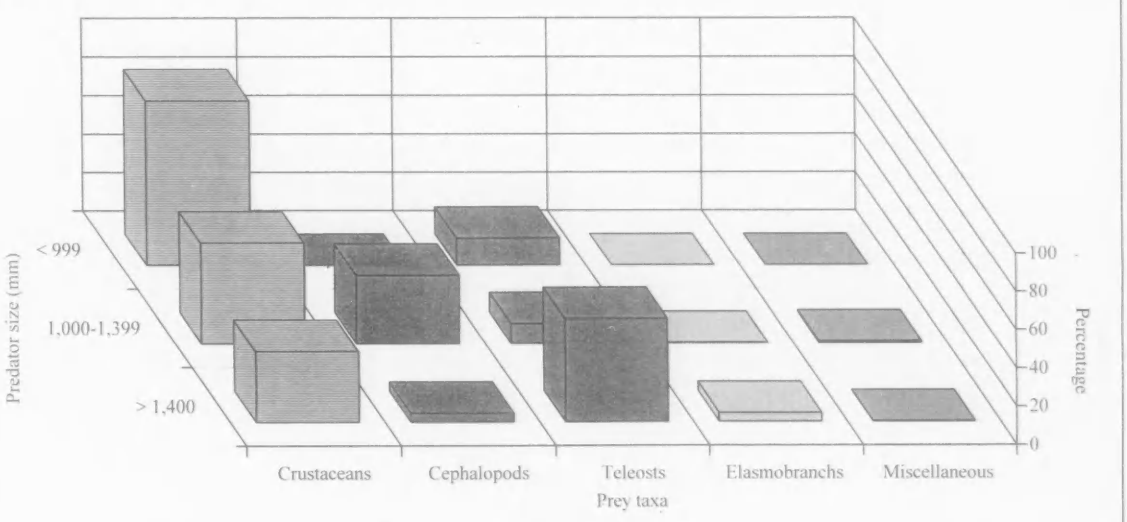

Figure 8

Percentage mass of different taxa in the diet for different size classes of *T. megalopterus*.

Table 1

Prey composition of three size groups of *T. megalopterus* from the Eastern Cape.

	< 999 mm TL			1,000–1,399 mm TL			> 1,400 mm TL		
	%F	%N	%M	%F	%N	%M	%F	%N	%M
Crustaceans									
Atergatis roseus							2.38	1	1.63
Ovalipes trimaculatus	4	1.89	0.27	4	1.39	0.02	9.52	5	1.83
Plagusia chabrus	76	69.81	78.29	60	50	48.48	30.95	16	16.26
Jasus lalandii							2.38	1	6.65
Panulirus homarus							4.76	2	4.78
Scyllarides elisabethae				8	2.78	1.72	11.90	6	4.65
Caridea	8	3.77	0.06				2.38	1	0.11
Unidentified crab spp.	20	13.21	7.18	16	8.33	2.45	9.52	5	0.86
Molluscs									
Cephalopods									
Loligo vulgaris reynaudii				8	2.78	7.83	2.38	1	0.96
Octopus vulgaris				24	13.89	25.48	7.14	3	1.72
Sepia sp.							2.38	1	0.01
Gastropods									
Haliotis midae				4	1.39	2.51	2.38	1	1.90
Teleosts									
Ariidae									
Galeichthys sp.							11.90	6	13.10
Carangidae									
Trachurus trachurus capensis				4	1.39	2.32			
Cheilodactylidae									
Cheilodactylus pixi	8	5.66	13	4	1.39	0.07	2.38	1	0.45
Chirodactylus brachydactylus				4	1.39	3.98			
Gobiesocidae									
Chorisochismus dentex							2.38	1	1
Haemulidae									
Pomadasys olivaceum	4	3.77	0.79						
Mugilidae									
Liza richardsonii							2.38	1	0.94
Platycephalidae							2.38	1	0.01
Pomatomidae									
Pomatomus saltatrix							7.14	2	0.70
Sciaenidae									
Argyrosomus inodorus				4	1.39	0.93	4.76	4	8.50
Sparidae							4.76	2	0.01
Diplodus sargus capensis	4	1.89	0.40	4	1.39	0.50	2.38	1	0.10
Lithognathus mormyrus							2.38	1	3.37
Pachymetapon aeneum							4.76	6	4.65
Pagellus bellottii natalensis				4	1.39	1.92	4.76	5	5.25
Sarpa salpa							2.38	2	2.76
Unidentified teleost remains				16	5.56	0.61	30.95	14	13.02
Elasmobranchs							2.38	1	0.18
Scyliorhinidae							2.38	1	0.16
Haploblepharus fuscus							2.38	1	0.94
H. fuscus (egg cases)				4	2.78	0.28	2.38	2	0.31
Rhinidae									
Rhinobatos sp.							2.38	1	2.65
Skate sp. (egg case)							2.38	1	0.31
Miscellaneous									
Bryophyte							4.76	2	0.02
Unidentified mussel				4	1.39	0.86			
Tapeworm				4	1.39	0.03			
Unidentified material							2.38	1	0.20
Total[1]	25	53	1092.64	25	72	3,014.90	42	100	4,898.95

[1] Totals are numbers of stomachs with prey, number of prey items, and prey wet mass (g).

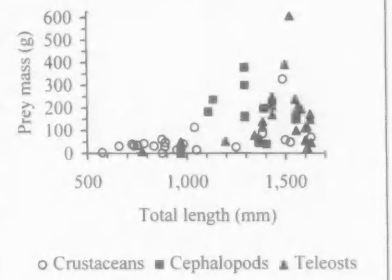

Figure 9

Calculated original prey mass plotted against *T. megalopterus* length, showing that the size of prey taken increases with predator size.

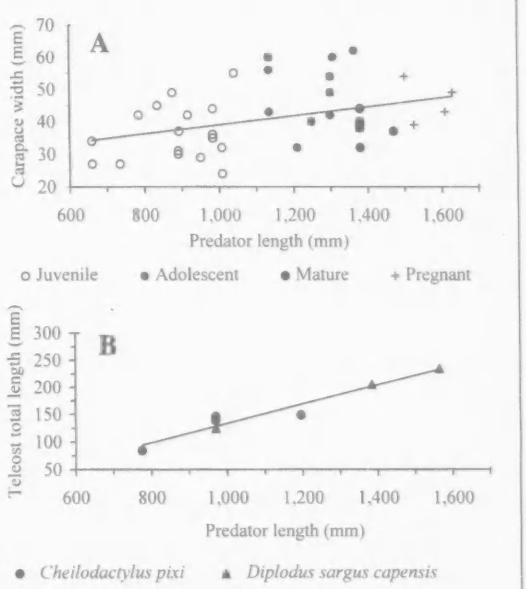

Figure 10

Relation between prey size and predator length. **(A)** *Plagusia chabrus* carapace width (CW) plotted against predator length. $CW = 25.1 + 0.014 \times TL$ (r=0.37, n=39). **(B)** Total lengths of two teleosts plotted against total length of the predator. The linear relation had the form TL (prey) = $-41.94 + 0.176 \times TL$ (predator) (r=0.97, n=7).

of a wide range of sizes, and there was a significant linear relation between crab carapace width and total length of sharks (r=0.37, P<0.05, n=39; Fig. 10A). Limited numbers of teleosts made analysis difficult. Combined data for two species (*Cheilodactylus pixi* and *Diplodus sargus*) showed a significant relation between the lengths of prey and sharks (r=0.97, P<0.01; n=7; Fig. 10B). The sample size of other prey species was too small to make similar analyses.

Discussion

Depth range

This study confirmed earlier reports that *T. megalopterus* prefers shallow rocky reefs (Bass et al., 1975; Compagno et al., 1989, 1991). They were found very rarely in deep waters, despite extensive sampling in deep waters for a variety of other sharks, including the closely related *Mustelus* species (Smale, 1991; Smale and Compagno, 1997). The nature of the samples precluded precise determination of intraspecific habitat choice, but there were no obvious differences in habitat choice by sharks of different sizes. The skewed sex ratio, which needs further investigation, may be due to sampling bias or social factors.

Reproduction

In *T. megalopterus*, eggs produced by the single functional ovary pass through the oviducal gland, where they are probably fertilized before they are enclosed in the membranous egg case. Embryonic development is ovoviviparous, embryos receiving nourishment from the yolk sac. However, some egg cases were slightly adherent and others intimately connected to the uterus wall. There was no evidence of the yolk sac forming a placental attachment at later stages of development, supporting Compagno's (1984) summary of the genus.

The size at which 50% of male sharks are mature is equivalent to mean size at maturity (Lenanton et al., 1990). Data from the present study indicated that males mature at approximately 1320 mm. Compagno (1984) estimated that males mature at 1300–1400 mm. On the basis of width of the oviducal gland and the diameter of the uterus and eggs, females begin to mature at about 1391 mm, and 50% maturity is achieved at about 1450 mm; all females larger than 1500 mm are mature. Compagno (1984) estimated that females mature between 1400 and 1500 mm and reported mature females of 1400–1740 mm. In this study, 50% maturity of female sharks is attained at about 1450 mm, which represents 70% of the maximum size observed, 2075 mm. This size falls within the range of 60%–90% noted by Holden and Raitt (1974). The smallest pregnant female measured 1465 mm.

Gestation in sharks is usually 10–12 mo and prolonged gestation periods are apparently rare, although *Squalus acanthias* has a gestation period of

22–24 mo (Wourms, 1977; Nammack et al., 1985; Hanchet, 1988; Wourms and Demski, 1993; Wourms, 1994). The gestation of frilled sharks, *Chlamydoselachus anguineus*, may be as long as three and a half years (Tanaka et al., 1990). The proposed gestation of about 20 mo in *T. megalopterus* is longer than the estimated 12 mo in *Triakis semifaciata* (Castro, 1983; Talent, 1985; Smith and Abramson, 1990). If the 20-mo estimate is correct, any females that mate shortly after parturition would have a resting period of two to three months. Some mature but nonpregnant females, however, show no sign of ovarian egg growth and development at the same time that others have large ovarian eggs or uterine eggs (or both) and small fetuses. These resting females represented 36% of the sample of 11 mature females taken between May and August. These females probably skip a year and have an extended reproductive break of at least 12–15 mo, which would prolong the cycle to at least 3 years for some individuals. On the other hand, some pregnant females about to undergo parturition have large ovarian eggs, and these individuals may mate within a few months and apparently forego the extended resting period.

On the basis of embryo growth rates presented above, mating and fertilization probably occur from about October to early December. Females carry term embryos of 422–440 mm (largest embryos) between the last week of May and the last week of August, which would approximate the time of parturition. Compagno's (1984) estimate of size at birth was much smaller (300–320 mm) than that of our findings. From observations of embryonic development, it was noted that during the late stages of embryo development (from ca. 400 mm), both external and internal yolks were absent. The small amount of yellow substance in the spiral valve was thought not to be an internal yolk reserve, but the area of absorption. It was also noted that each embryo was contained in a soft egg case with ca. 500 mL of fluid (Goosen, 1997). Wourms and Demski (1993) noted that in *Squalus acanthias*, several months into the 22-mo gestation period, embryos can ionoregulate and osmoregulate in a uterine solution resembling seawater. This might be the case for *T. megalopterus* and could contribute to near-term embryo nourishment until parturition occurs.

The liver mass of a shark is a good index of the shark's condition (Springer, 1960). In our study it was found to fluctuate widely, particularly after maturation. Seasonal variation in HSI of the lesser sandshark (*Rhinobatos annulatus*) has been attributed to fluctuations in lipid content of the liver, which has been correlated with reproductive condition in females (Rossouw, 1987). Similar changes in HSI have been recorded in pregnant females of three *Mustelus* species (King, 1984; Smale and Compagno, 1997). Although low HSI values were found in pregnant females with near-term embryos in this study, the relation was not statistically significant, possibly suggesting that HSI fluctuates with other physiological factors. These observations were based on a small sample size and need further investigation.

Feeding

This study showed that *T. megalopterus* changes diet with growth, which suggests that it selects prey of suitable size. Because there is no evidence to date of marked habitat change with growth, and all sizes of shark do not have the same prey, it is unlikely that they are feeding opportunistically, even if they favor abundant species. Opportunistic feeding *sensu* Wetherbee et al. (1990) implies that stomach contents are varied but of composition and abundance similar to those of prey in the environment. Smale (1996) noted that the term "opportunistic" should be used with caution because it is difficult to distinguish between abundance and availability. Ontogenetic variation in feeding of *T. megalopterus* appears to be attributable to broadening the diet to include more energetically rewarding species (e.g. teleosts), although benthic prey are still taken.

Spotted gully sharks fed primarily on the crab *Plagusia chabrus*; as sharks grew, larger individuals were taken. This finding conforms with those where large crabs were taken by larger leopard sharks (*T. semifasciata*; Talent 1976). Although spotted gully sharks are most abundant near reefs, they may also hunt over sandy areas to exploit the crab *Ovalipes trimaculatus,* which prefers sandy substrates. Spotted gully sharks preyed largely on nocturnally active lobsters (Paterson, 1969; Smale, 1978; Zoutendyk, 1988) and crabs (Brown, 1961; Warner, 1977), suggesting that they are nocturnal hunters that take crustaceans as they emerge. Such activity may explain why anglers catch them more frequently at night.

As the sharks increase in size, they use a much wider variety of prey groups, including teleosts. Therefore, with growth the spotted gully shark is able to attack and ingest larger prey species. Nocturnally hunting sharks may be able to take some teleosts when they are less active or resting at night. Elasmobranchs became increasingly important prey with growth, a finding that supports previous observations of congeners taking elasmobranchs (Bass et al., 1975; Russo, 1975; Talent, 1976; Compagno, 1984).

Octopus vulgaris was the most common cephalopod prey. It inhabits reefs (Smale and Buchan, 1981; Roper et al., 1984) and emerges from its den to hunt

between dusk and dawn (Smale and Buchan, 1981), making it vulnerable to nocturnal predators. Squid (*Loligo vulgaris reynaudii*) is common throughout the Agulhas Bank (the continental shelf between Cape Town and Port Elizabeth) but become concentrated inshore in spring and early summer, when it spawns (Sauer and Smale, 1991; Augustyn et al., 1992). Egg laying is concentrated on the bottom during the day in waters 10–50 m deep (Augustyn, 1990; Sauer et al., 1997). Squid are thought to be especially vulnerable to predation during mating and spawning (Smale, 1991; 1996). Sauer and Smale (1991) recorded *T. megalopterus* as one of the squid predators in the vicinity of spawning aggregations, which illustrates its ability to exploit a superabundant prey resource by day, even though it normally appears to hunt at night.

In conclusion, it is evident that the habitat preferences of gully sharks make them vulnerable to exploitation by inshore fishermen. Their life history traits—large size at maturity, prolonged gestation period, and relatively small litter size—suggest that this species is unsuitable for sustained harvesting by either recreational or commercial fishing.

Acknowledgments

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Behavior of winter flounder, *Pseudopleuronectes americanus*, during the reproductive season: laboratory and field observations on spawning, feeding, and locomotion

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Abstract.—Continuous observations in a large research aquarium (121 kL) over a 14-week period were combined with field collection in the Navesink River estuary, New Jersey, to explore the behavior of winter flounder (*Pseudopleuronectes americanus*) during and after the spawning season. Ten males and ten females held in the aquarium spawned over a 60-day period, with an average of 40 spawns per female and 147 spawns per male. Males initiated all observed spawning events, which occurred throughout the night, but primarily between sunset and midnight. Spawning by one pair frequently elicited sudden convergence and spawning by secondary males (up to six individuals); consequently, strictly paired spawning was uncommon (22% of events). Males and females were almost entirely nocturnal during the reproductive season but became increasingly diurnal during the postspawning season.

Males and females arrived in the estuary in ripe spawning condition; fish with high gonadosomatic indices were collected during most of February and March 1997. All of the ripe females were >20 cm in total length and at least two years old, whereas ripe males measuring 10–15 cm were common. Ripe males were found throughout the system whereas ripe females were concentrated in the middle reach of the estuary. Field collections revealed that females began feeding, primarily on ampeliscid amphipods and on siphons of the clam *Mya arenaria* earlier in the season than males. Males in the laboratory also began feeding late in the season, after most spawning had ended. Field and laboratory results combine to indicate that male spawning strategy is adapted to maximize numbers of eggs fertilized. There is probably high genetic diversity in the offspring from any one female owing to frequent spawning and to multiple males participating in individual spawning events.

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Winter flounder, *Pseudopleuronectes americanus*, is an important commercial and recreational fishery species in estuarine and continental shelf habitats along the Atlantic coast of North America from Labrador to Georgia (Scott and Scott, 1988). A large number of investigations have been devoted to this species and its life history is relatively well known (Klein-MacPhee, 1978; Able and Fahay, 1998). Winter flounder populations include several substocks that mix during summer residence on the shelf, but adults return to natal estuaries to spawn (Saila, 1961; Poole, 1966; Howe and Coates, 1975; Pierce and Howe, 1977; Phelan, 1992). In the Mid-Atlantic Bight, adults make seasonal migrations into the estuaries of New York and New Jersey (Perlmutter, 1947; Phelan, 1992) where they spawn in shallow inshore waters during late winter (Scarlett and Allen, 1992).

Winter flounder in the mid-Atlantic region are believed to mature at 2–3 years, at 20–25 cm total length (Perlmutter, 1947, Danila, 1978; Witherell and Burnett, 1993). Considerable attention has been given to seasonal movement (Perlmutter, 1947; Saila, 1961; Howe and Coates, 1975; Phelan, 1992) and to fecundity and reproductive state in wild populations (Kennedy and Steele, 1971; Danila, 1978; Burton and Idler, 1984; Nelson et al., 1991); however, information on spawning behavior is limited to observations made by Breder (1922) of fish in small laboratory tanks.

In this investigation we expanded Breder's (1922) description of spawning and courtship in winter flounder by making continuous observations on a population of winter flounder in a large research aquarium for a 14-week period during and after the reproductive period. We determined the total number of spawning events for males and females in the population and examined seasonal and diurnal variation in spawning, feeding, and locomotory activity. On the basis of field collection we described population structure, gonadal development, feeding, and localized movements by a wild population of winter flounder in an

estuarine spawning ground during winter and spring 1997.

Methods

Laboratory observations

Experimental animals Winter flounder were collected in nearshore waters between Rockaway Point and Coney Island, New York, on 27 January 1997 with a 9.2-m otter trawl fished from RV *Gloria Michelle*. Flounder were held in live cars with flow-through seawater and transported in large ice chests to the laboratory. Mature ripe males were identified by the extrusion of sperm under light pressure applied to the body. Females were identified by the presence of full ovaries distending the body, occupying a large portion of the body cavity, and extending almost to the caudal peduncle. Ten males and ten females, each greater than 200 mm in TL (total length), were marked with Peterson tags (13 mm diameter) before release into the research aquarium. To provide visual identification of gender on videotape, males and females were marked with orange and white tags, respectively. These colors were distinguishable with low-light video cameras during both day and night. At the beginning of the experiment the mean total length of male flounders was 29.8 cm (SD=3.2, range=24.3–34.4 cm). Mean length of females was 28.5 cm (SD=2.6, range=23.5–30.8 cm). Four fish (two males and two females) died near the end of the 14-week observational period; these were not replaced. The fish were remeasured for total length at the end of the experiment to estimate growth.

Research aquarium Observations of the winter flounder were made in the research aquarium at the James J. Howard Marine Sciences Laboratory at Sandy Hook, New Jersey. The aquarium (121 kL volume) is an oval 10.6 m long, 4.5 m wide, and 3 m deep, with eight rectangular windows (0.7 m wide and 1.2 m high), one in each end and three along each side. There is a recirculating system so that 10% of the water is replaced each week. Seawater upwells through coarse sand which covers the bottom of the aquarium (46 m^2) to a depth of 40 cm, then exits through drains at the top of the tank.

For this experiment, photoperiod in the aquarium room, which was controlled by a computer-driven bank of fluorescent lamps (Duro-Test, Vita-Lite: model CRI91; 5500°K), was programmed to follow the natural sequence at the location of the laboratory (40°28'N, 74°00'W), with a 13.5-h dark period at the end of January, when fish were first introduced into the system, and a 10-h dark period at the end of the study in mid-May. During nighttime hours, light intensity on the sediment surface was 0.17 lux (1.98×10^{-6} mEinsteins PAR [photosynthetic active radiation]). Light intensity increased at the time of twilight to 2.0 lux (2.92×10^{-5} mEinsteins PAR) for 20 min, followed by a natural rise in intensity to 206 lux (0.0027 mEinsteins PAR) at midday. Return to nighttime conditions followed an exact reverse pattern.

Water temperature was held at 4.0°C (±0.5°C) from the beginning of the observations until 27 March, when a cooling system malfunction allowed temperature to rise to 7.5°C. To follow conditions in the Navesink River, we held water temperature at 7.5°C until 10 April, then raised temperature ~0.5°C per day to 15°C on 14 April. This temperature was maintained until the end of observations on 13 May 1997.

Finely chopped pieces of frozen surf clam (*Spisula solidissima*) were made continuously available as food for the flounders. The food was renewed at least once per week during the early part of the period when feeding was light, and increased with ingestion rate to near-daily additions by 1 April 1997. The food was placed on the bottom in an area approximately 2 m in diameter within camera view so that all feeding bouts could be counted.

Recording observations Two low-light-sensitive video-tape cameras were set at the end windows of the aquarium to make continuous recordings of courtship and spawning events over a large portion of the tank from bottom to water surface. Each of these cameras viewed 53% (24.6 m^2) of the tank bottom with minimal overlap in coverage. Recordings were made from about 1530 h through 0500 h between 29 January and 18 April 1997, after preliminary taping and routine visual observation indicated that virtually all activity was nocturnal. The validity of this approach was confirmed by cameras at the side windows set for 24-h recording throughout the study period. Twenty-four-hour recording from the end cameras was initiated 19 April 1997, concurrent with increasing daytime activity of the fish.

Spawning events were divided into two classes. An event was considered "definite" when characteristic behavior patterns were clearly observed in the recorded image. However, because most spawning occurred in darkness, some spawning events were not observed clearly. These likely but less certain spawning events were scored "probable." Two forms of courtship were recorded; these are described in the "Results" section. Records were kept of the numbers of males and females involved in each courtship and spawning encounter. A feeding event was scored once,

regardless of feeding duration, when a fish entered the food distribution area and made obvious feeding motions toward the clam pieces. Analysis of video tape from the two cameras for four dates during midspawning season revealed that there were no significant differences in daily counts of spawning, courtship, and feeding as recorded by the two cameras (paired-sample t tests, $P>0.30$); therefore, the second camera was used only as a backup for recorder failure (e.g. on four dates).

Two other low-light cameras were set at side windows to provide data on locomotory activity and swimming speeds. Each viewed a 3.6-m wide section of the opposite tank wall and about 4.6 m^2 of bottom, and recordings were made for 5 min at the beginning of each hour. An index of locomotory activity was provided by the number of fish passing a central line in view of the camera. Swimming speeds (cm/sec) were determined by timing the passage of fish between two points 142 cm apart on the tank wall. Whenever possible, the gender of fish passing through this view was noted. The two cameras provided essentially identical information, and recordings from only one were analyzed for each day.

Observations were also made on the relative abundance of winter flounder larvae in the aquarium. Flounder larvae were almost constantly present in the aquarium after mid-February, and an index of their abundance was recorded each day. Because the larvae demonstrated diurnal vertical migration, observations were made at approximately 1200 h and general abundance was scored from zero to four. A score of one was recorded when only a few larvae were observed in any field of view and a score of four was given when thousands of larvae were present at all of the tank windows.

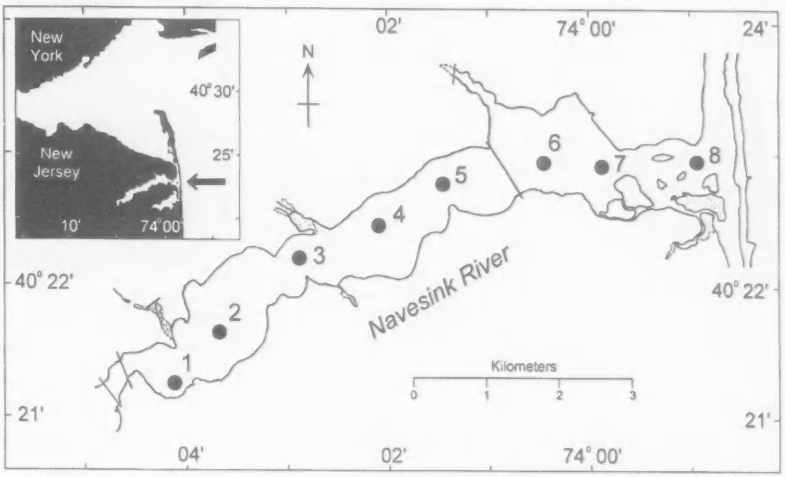

Figure 1

The Navesink River estuary, New Jersey, showing the stations where collections were made for winter flounder during winter and spring 1997.

Field collections

To monitor the location, reproductive condition, and sex ratio of winter flounder in a wild population, weekly daytime otter-trawl surveys were conducted from 7 February to 24 April 1997 in the Navesink River estuary, New Jersey (Fig. 1), which is a known spawning area for the species (Scarlett[1]). Eight fixed stations were established approximately 1 km apart throughout the system. Two 5-min tows (at 4.4 ±0.9 km/h) were made at each station with a 5-m semi-balloon otter trawl with 3.5-cm wings and body and a 6-mm codend liner. Abundance of winter flounder was reported in catch per unit of effort standardized as number of individuals per 100 m of tow distance, which was estimated with a global positioning system (GPS).

Winter flounder collected in the trawl surveys were measured to the nearest millimeter of total length, blotted dry, and weighed to the nearest gram. Gender was determined by inspecting the gonads, and each fish was classified as immature, ripe, or spent. The gonads were weighed to the nearest gram, and gonadosomatic indices (GSI) were calculated according to LeCren (1951) as

$$GSI = 100\ (gonad\ weight/total\ body\ weight).$$

The stomach of each winter flounder was removed, preserved in 10% formalin solution, and later transferred to 70% ethanol. Diet was analyzed as in Stehlik (1993), and fullness of the foregut was estimated visually on a scale from 0% to 100%. Prey items were identified to the lowest possible taxon and the proportion of the total volume of stomach contents con-

[1] Scarlett, P. G. 1991. Temporal and spatial distribution of winter flounder (*Pseudopleuronectes americanus*) spawning in the Navesink and Shrewsbury Rivers, New Jersey. Dep. of Environmental Protection, Div. Fish, Game and Wildlife, Bureau of Marine Fisheries, Nacote Creek Marine Fisheries Laboratory, Star Route, Absecon, New Jersey, 12 p. Unpubl. report.

tributed by each prey type was estimated visually (Williams, 1981). Fullness was averaged for fish grouped by date, gender, and stage of reproductive development. Fish examined were 63–460 mm TL.

Bottom water temperature, salinity, and dissolved oxygen were measured weekly at each station with YSI (Yellow Springs Instruments) oxygen and temperature-conductivity meters. HydroLab DataSonde II instruments were deployed near the bottom on piers extending from the south shore of the Navesink River near stations 1 and 6 to record temperature, salinity, and dissolved oxygen each hour.

Results

Laboratory observations

Behavior Two forms of simple courtship behavior were observed in the research aquarium: "following" and "avoidance." "Following" was defined as oriented locomotion of one or more fish behind another, typically on the sediment surface. A following could be relatively slow or fast (approx. 20–50 cm/sec), continued for 5–20 sec, and sometimes resembled chasing. Turns by the lead fish were followed by the fish behind, and, in most cases, the distance between fish decreased but contact was never made. In all cases where genders of the fish could be determined the lead was female. One or more "followers" were always male. "Avoidance" was characterized by brief contact (<1 s) between a "follower" and the female being followed, then by rapid acceleration and evasive turning by the female. Typically, the female swam 1–2 m off the bottom. In at least 50% of such encounters additional males converged rapidly on the female, eliciting strenuous evasive swimming by the female.

Our observations of spawning in winter flounder were relatively similar to those of Breder (1922), except that females never initiated spawning. Spawning occurred after initial contact by a male as described above. Instead of fleeing, the female remained near the sediment surface (<1.0 m above it) and the pair immediately made several very rapid circles with diameters typically less than two body lengths. Spawning events could be detected even in the far reaches of the tank during darkness because the female nearly always rotated momentarily to the vertical position so that the white underside of her body was clearly visible on the outside of the circles. Participation by multiple males in the spawning event was common, and in approximately 10% of spawning events, one to several males converged on the spawning location immediately after the female had departed, making rapid undulating motions on the sediment surface. Despite convergence of males on spawning females and spawning locations, agonistic behavior among males was never observed. In less than 2% of observed spawning events, a second spawning by the same female occurred a short distance from the first encounter. In most cases the female avoided further contact.

Spawning Spawning began on 8 February 1997, about 2 weeks after the fish were introduced into the research aquarium. One or more spawnings occurred in camera view every day, except 14 February, until 1 April (Fig. 2A); maxima were evident in mid-February and mid-March. The last spawnings were observed on 8 April. In total, 211 spawning events were recorded, 34% of which were definite. In analyses that follow, we considered the "spawning season" in the aquarium to be the period between 8 February and 8 April, 1997. The "postspawning season" was the remainder of the observational period, 9 April through 13 May 1997.

Spawning began near or just before sunset (1700–1800 h) and reached maximum frequency around 2100 h (Fig. 3A). Seventy-five percent of all observed events occurred before midnight. Although some spawning occurred as late as 0430 h, only 10% occurred after 0200 h, when the fish became relatively inactive.

When the total number of spawning events during the observation period was extrapolated to the total dimensions of the aquarium and divided by the ten females in the system, we estimated that the average female flounder spawned 40 times during the reproductive season. It is unknown whether individual fish spawned over this extended observation period. However, given that the mean total number of spawns per night was just six, individuals probably spawned over a period of at least one week. Two facts suggest that a subset of the females may have been completely spent during the first three weeks of the spawning period: the nightly spawning frequency was bimodal, with a minimum on 2 March (Fig. 2A), and female feeding increased rapidly after approximately 3 March (Fig. 4).

None of the observed spawning events involved more than one female flounder, but multiple males were engaged in the majority of spawnings. In 151 events with records for the number of males, only 22.5% were pair spawnings, 11.3% had two males, 3.3% had three males, and the majority involved four to six males (62.9%). Given these numbers, a conservative estimate for the total number of male spawnings within camera view is 780. By extrapolating to total tank dimensions and dividing among the ten males

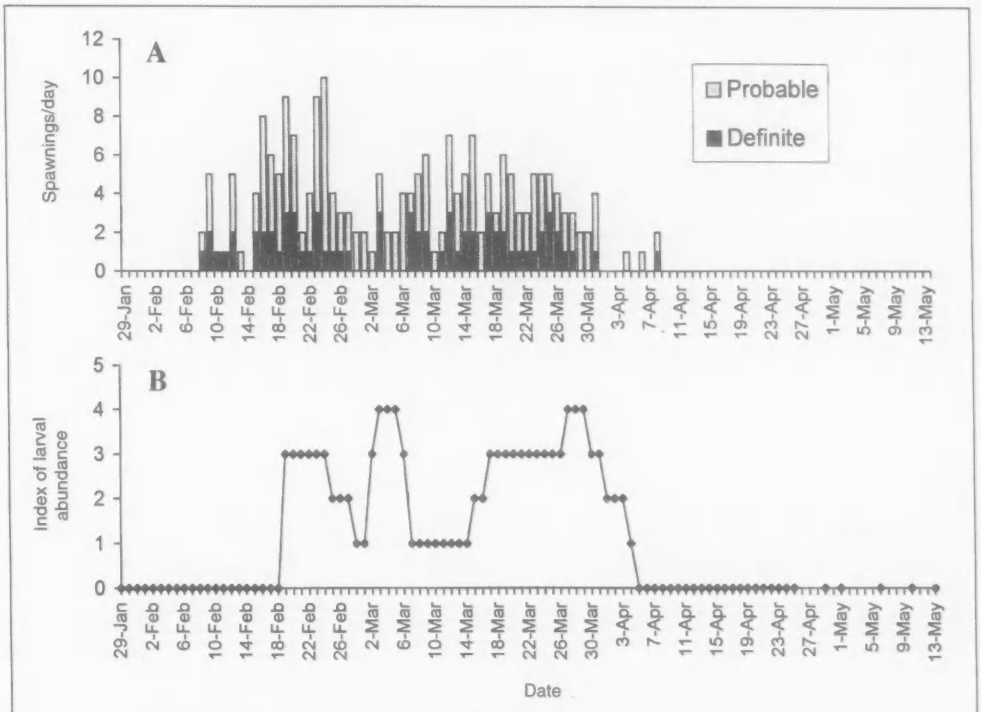

Figure 2

(A) Number of winter flounder spawnings observed on a daily basis in the research aquarium. **(B)** Larval abundance in the research aquarium as a function of date. The index represents only newly hatched larvae because older larvae were extracted by aquarium filtration.

in the system, we estimated that each male (on average) spawned approximately 147 times during the season.

Larval abundance The first winter flounder larvae were observed in the aquarium on 19 February, 11 days after the first spawning was observed. A week of low larval abundance occurred in March, but larvae were constantly present until 5 April (Fig. 2B). Because there was no appreciable food for fish larvae in the aquarium, most of the larvae observed were at yolksac and early stages.

Courtship behavior The spawning season was characterized by a high frequency of following behavior (Fig. 5A). Only a small amount of following was observed in the days before and after the spawning season, but 50–200 following events were observed each night between 8 February and 8 April, decreasing steadily after mid-March. This pattern reflected spawning frequency (Fig. 2A), and there was a weak but positive correlation (r=0.531, P<0.001) between the two forms of behavior.

Avoidance events were approximately one order of magnitude less frequent than following events (Fig. 5), but the seasonal patterns were similar, and there was a positive correlation between these behaviors (r=0.786, P<0.001). The correlation between avoidance and spawning was also positive (r=0.441, P<0.001). Most courtship behavior occurred after sunset between 1700 and 0400 h, with a broad mode around 2100 h (Fig. 3, B and C). Very few interactions occurred in daylight.

Feeding and growth The seasonal pattern of feeding was entirely different from the patterns of spawning, following, and avoidance behaviors. First feeding occurred on 10 February, then increased slowly over time—some apparent oscillations, however, were embedded in the overall trend (Fig. 4). For example, an approximately 10-day periodicity occurred between 12 February and 20 March; this was independent of the dates when fresh food was added. All feeders that could be identified prior to 18 March were female. Females were responsible for 90% of all feeding events recorded (n=3673), and this percentage

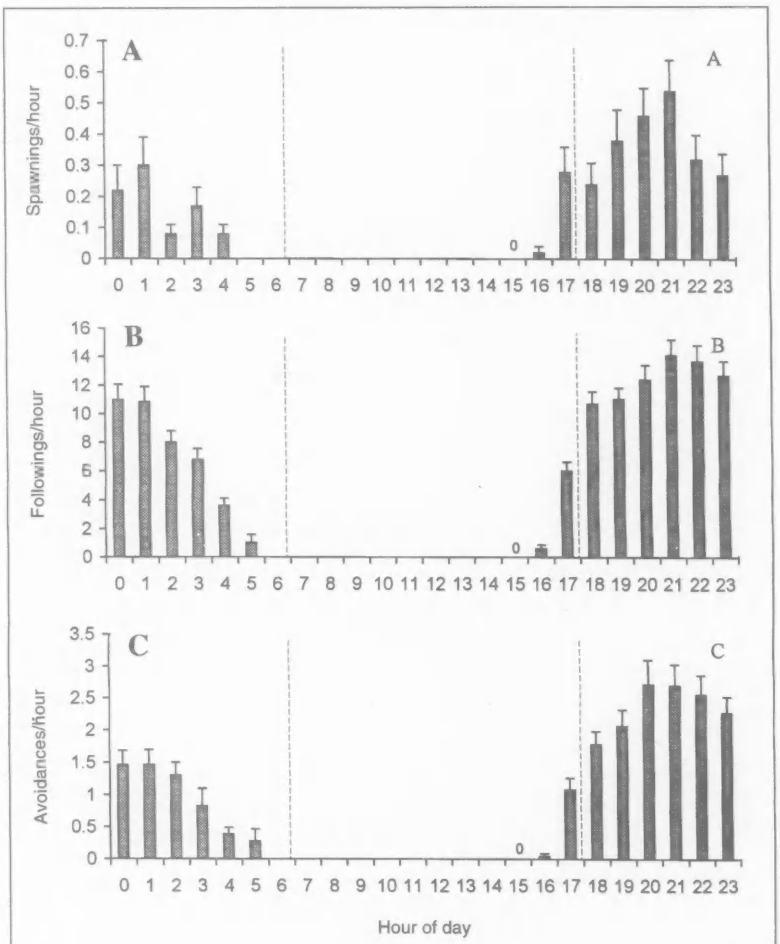

Figure 3

Hourly frequency of **(A)** spawning, **(B)** following, and **(C)** avoidance behavior by winter flounder during the spawning season in the research aquarium. Values represent mean numbers of observed events per hour ±1 standard error. The dashed vertical lines show the times of artificial sunrise and sunset in the aquarium at the midpoint of the spawning season. Photoperiod was maintained on a natural cycle for the latitude of the laboratory.

did not differ appreciably between spawning (90.3%) and postspawning (89.8%) periods.

It is possible that feeding frequency was related to water temperature. During the time when water temperature was 4°C (until 25 March), average feeding frequency was 14 bouts/day (SD=17, n=45). During the period when temperature was 9°C (26 March–8 April), feeding frequency increased to 94 bouts/day (SD=47, n=11), and when the temperature was 15°C (14 April–13 May) there were 159 bouts/day (SD=107, n=17).

Diurnal feeding periodicity was similar in males and females. During spawning season, most feeding occurred in the hours immediately following sunset and ended before sunrise (Fig. 6, A and C). After spawning ended, feeding (particularly by females) was dispersed throughout day and night, and maximum feeding occurred from afternoon to early evening, primarily 1300–1900 h (Fig. 6B). The least feeding activity occurred from approximately midnight until 1100 h. Feeding by males during the postspawning season continued to be much less frequent than feeding by females; however, the diurnal pattern shifted similarly to an earlier period of maximum activity (Fig. 6D).

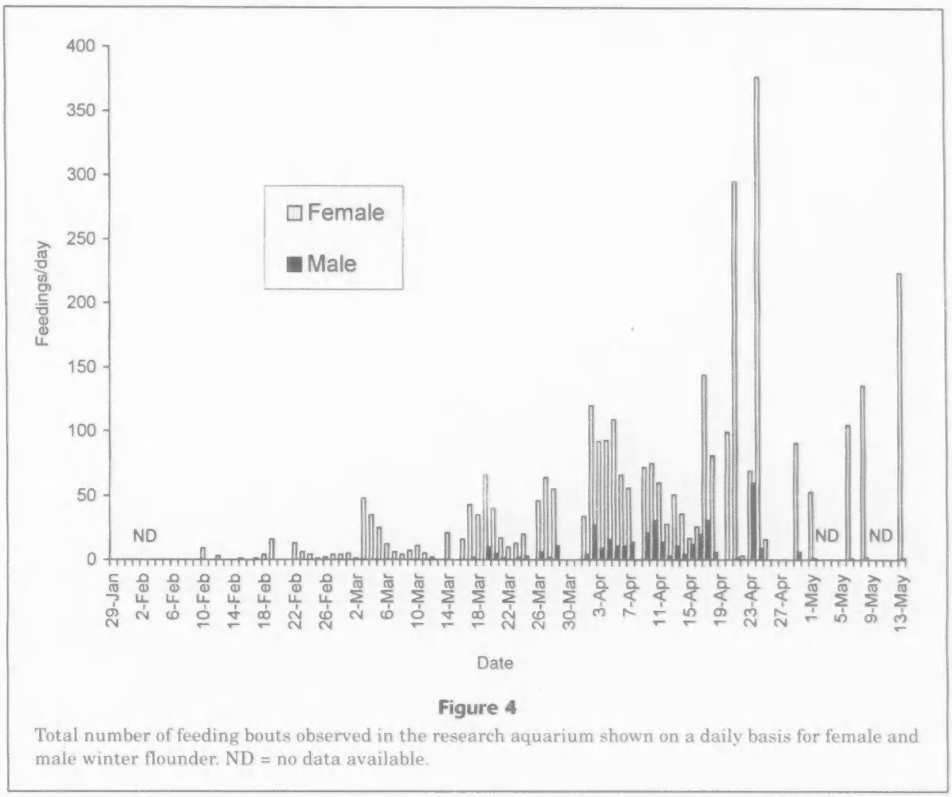

Figure 4

Total number of feeding bouts observed in the research aquarium shown on a daily basis for female and male winter flounder. ND = no data available.

Most female winter flounder demonstrated growth in total length (mean=1.0 cm, SD=1.0) during the three-month experimental period, despite the cold temperature and high spawning activity. Change in length of males (mean=0.1 cm, SD=0.6) was less but the gender difference was not significant (Student's t=–1.91, df=7, P<0.098) because of large individual variation.

Locomotory pattern General activity in winter flounder during the spawning season began near sunset and remained high throughout the night until sunrise (Fig. 7, A and C). After spawning ended, approximately equal levels of activity were observed during day and night, with highest levels during afternoon and evening hours. Diurnal patterns of locomotion were somewhat different in males and females. During the spawning season, male fish began moving somewhat earlier in the evening than females, and the general level of activity was higher. Postspawning, female fish shifted more strongly to an afternoon activity pattern whereas males continued a high level of activity into the night and early morning hours (Fig. 7).

Swimming speeds of winter flounder were generally near 20–25 cm/sec, and there was no apparent effect of date or time of day during active hours. However, male fish were significantly faster (overall mean=26.1 cm/sec, SD=6.6) than females (mean=21.2 cm/sec, SD=4.6; Student's t=14.61, P<0.001).

Field observations

Physical conditions Temperature in the Navesink River estuary ranged from 2.2°C in mid-February to 11°C at the end of the field study in late April, and there was relatively little temperature variation among the eight field stations (Fig. 8A). Salinity near station 6 in the eastern part of the study area ranged from 15 to 23 ppt over the study period. At station 1 in the western part of the study area, salinity was 10–21 ppt, except for a brief period of low salinity (7–10 ppt) on 1 April 1997. Therefore, the entire sampling area was polyhaline, and there was a slightly wider range of salinity in the west than in the east. Dissolved oxygen was always high (>8 mg/L) at the two sites where measurements were made continuously.

Population structure, reproduction, and migration Numbers of winter flounder in the Navesink River

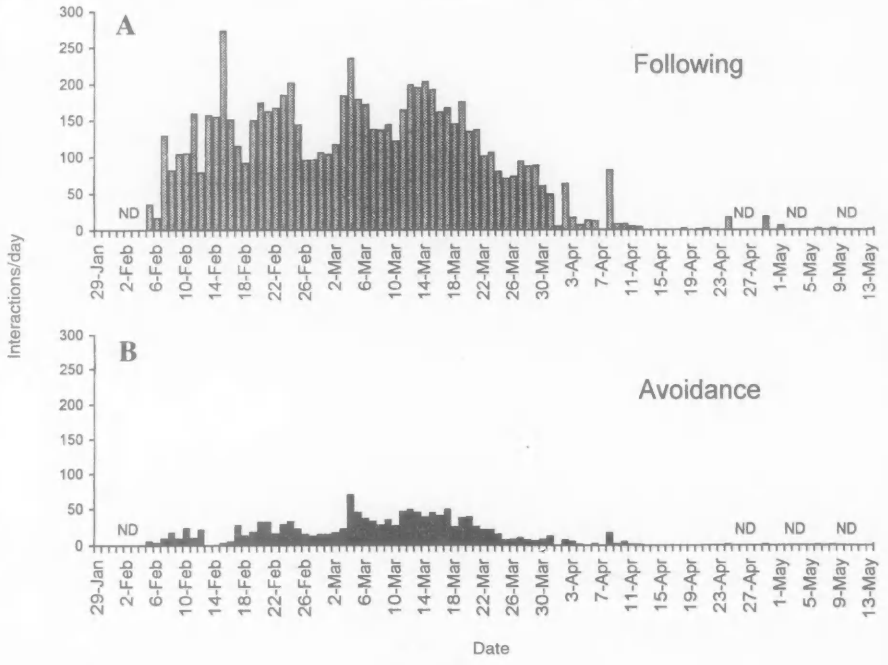

Figure 5

Daily frequencies for **(A)** pursuit and **(B)** avoidance behavior exhibited by adult winter flounder in the research aquarium.

estuary increased steadily between mid-February and early March, concurrent with the rise in water temperature (Fig. 8). Abundance remained relatively stable for the remainder of the collection period. Of the 389 winter flounder collected, 49% were female (mean length=28.9 cm, SD=8.9) and 32.5% were male (mean=25.1 cm, SD=6.9). Gender could not be determined for 18.5%, all of which were small individuals considered to be age-1 fish (mean=10.2 cm, SD=2.3). Females were significantly more abundant than males (Table 1; F=4.62, P<0.05), with a sex ratio of 1.5 to 1, and this pattern was consistent throughout the sampling period; analysis of variance (ANOVA) showed a nonsignificant *Date × Gender interaction* (P=0.58; Table 1).

The majority of ripe female flounder were collected in the first half of the survey period (Fig. 9A); all of these fish were larger than 20 cm TL. Ripe females were divided into two obvious groups based on gonadosomatic index (GSI). Sixty-five percent of ripe females had GSIs greater than 20% (mean=30.9, SD=9.1). A second group of nearly spent females had GSIs of 3–8%. All female winter flounder collected after mid-March had GSIs less than 6%.

Table 1

Results of analysis of variance on catch data for winter flounder in the Navesink River during winter 1997. ANOVA was performed on natural log-transformed data on catch per unit effort. *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; ns = $P > 0.05$.

Source of variation	df	Sum of squares	F ratio
Date	9	0.002	3.27 **
Station	7	0.004	7.25 ***
Gender	1	0.0003	4.62 *
Date × Station	63	0.009	2.10 ***
Date × Gender	9	0.0005	0.84 ns
Station × Gender	7	0.004	7.22 ***
Date × Station × Gender	63	0.003	0.59 ns
Error	160	0.011	

Male winter flounder formed two size groups, small fish (<20 cm TL) assumed to be age-1 fish and larger individuals (20–35 cm TL). Through the end of February all males larger than 20 cm were reproduc-

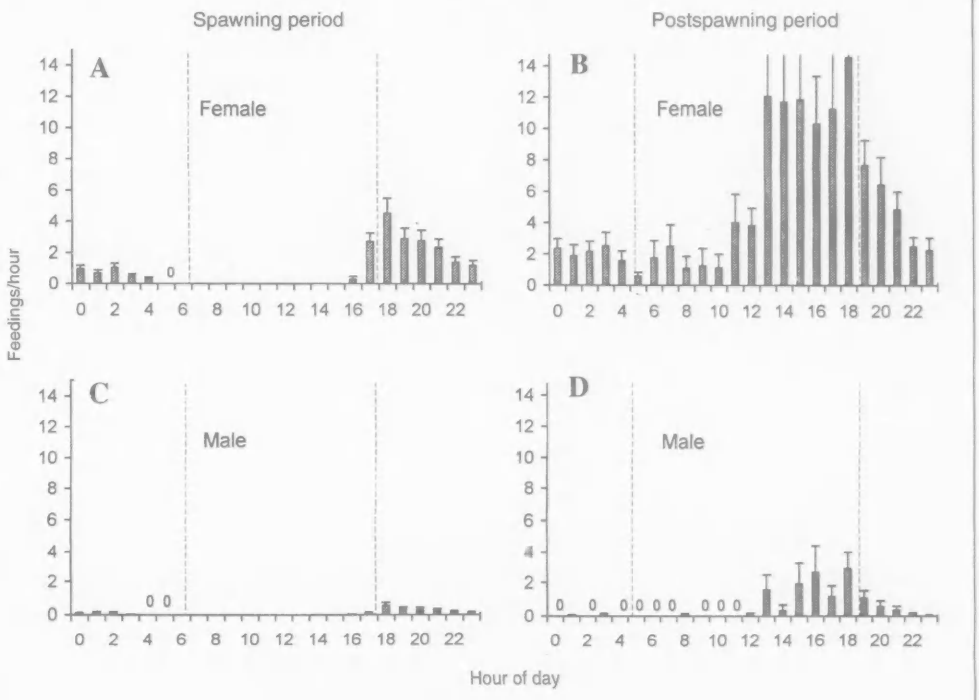

Figure 6

Hourly frequency of feeding during spawning and postspawning periods for **(A, B)** female and **(C, D)** male winter flounder in the research aquarium. Values represent mean numbers of observed events per hour ±1 standard error. The dashed vertical lines show the times of artificial sunrise and sunset in the aquarium at the midpoint of the spawning season. Photoperiod was maintained on a natural cycle for the latitude of the laboratory.

tively ripe, as were 40% of males between 10 and 15 cm. A steady decline in male GSI began in March (Fig. 9B), but ripe males (mean GSI=7.3, SD=4.4) were collected later than ripe females, through 11 April.

Although the number of fish collected at any one station was not large, the *Station* × *Gender interaction* in the ANOVA indicated that male and female flounder had different distributional patterns in the estuary (Table 1). Males were more abundant than females at stations in the lower estuary (stations 7 and 8), whereas females were more abundant in the middle and upper reaches (stations 1–6) (Fig. 10). These gender-specific distribution patterns were generally consistent, as indicated by the nonsignificant *Date* × *Station* × *Gender* interaction term in the ANOVA (Table 1). Ripe males were collected throughout the estuary in proportions ranging from 14% of individuals at station 6, to 100% at stations 1 and 2. In contrast, all ripe females were collected at stations 1–4, with the exception of one partially spent female collected at station 7.

The length distribution of female winter flounder at most of the sampling stations showed two modes (Fig. 11). Large females (mean length=29.7 cm, SD=0.6) were collected at all eight stations but were most abundant in the middle reach (stations 3–6). Small females (<20 cm TL), all of which were reproductively immature, were most abundant in the upper estuary, with approximately equal numbers of small fish at stations 1–4. Size groups were less obvious in male winter flounder (Fig. 11), but it is clear that the mean size of male fish was larger at stations in the lower river (stations 5–8) than in the upper river, and small fish were most abundant at stations 1–3. From 28 March through the end of the sampling period, large numbers of flounders were collected only at station 6. Virtually all the fish in the lower river during this late part of the collecting season were spent.

Feeding Stomach fullness in winter flounder varied with date, gender, and age (Fig. 12). Highest full-

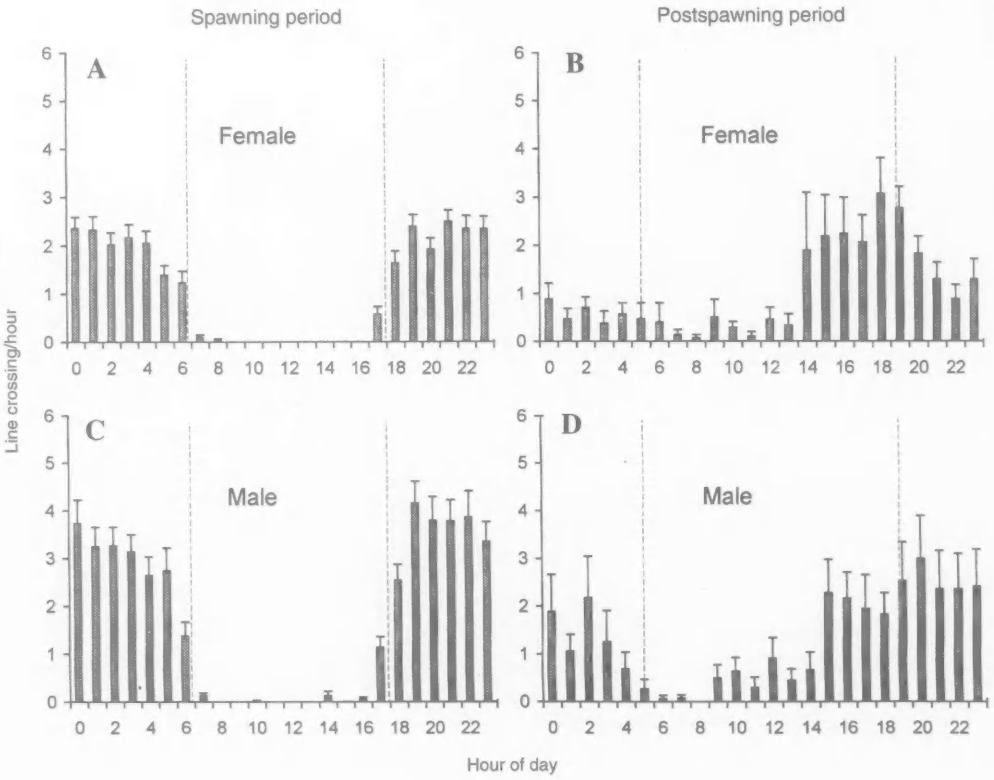

Figure 7

Locomotory activity in adult winter flounder in the research aquarium shown on an hourly basis for **(A, B)** females and **(C, D)** males during the spawning and postspawning periods. See text for the method used in generating this index of activity. The dashed vertical lines show the times of artificial sunrise and sunset in the aquarium at the midpoint of the spawning season. Photoperiod was maintained on a natural cycle for the latitude of the laboratory.

ness indices (59%–84%) occurred in immature fish, most containing substantial amounts of food. Average fullness in females was also high throughout the survey period (60%–80%), but variation was large and associated with reproductive state. Ripe females had an average fullness of just 24%, whereas spent females had an average fullness of 72%. Variation among males was even higher, with an obvious increase in fullness from about 1% early in the survey to a range of 70%–90% during the last three collection dates (Fig. 12). Ripe males had average stomach fullness of only 17%, whereas average fullness of spent males was 69%. Therefore, the rapid increase in stomach fullness of males in late March was associated with rapidly declining numbers of ripe males. Stomach fullness was weakly correlated with GSI in both females (r=–0.439) and males (r=–0.582) because fullness in fish with a low GSI spanned the entire range from 0%–100%.

Siphons of soft clam (*Mya arenaria*) were the most abundant prey items taken by winter flounder, on the basis of both percentage volume and frequency of occurrence. Of the 257 flounders that contained prey, 150 contained siphons with diameters of 3–13 mm. However, diet varied with collection site (Fig. 13). Siphons of *M. arenaria* were most abundant in fish collected in the middle reach of the estuary (stations 3–6), whereas another clam, *Macoma balthica*, was most abundant in fish from the upper reach (station 1). Ampeliscid amphipods, mysids, shrimps, and other crustaceans were the most important food items in the lower estuary.

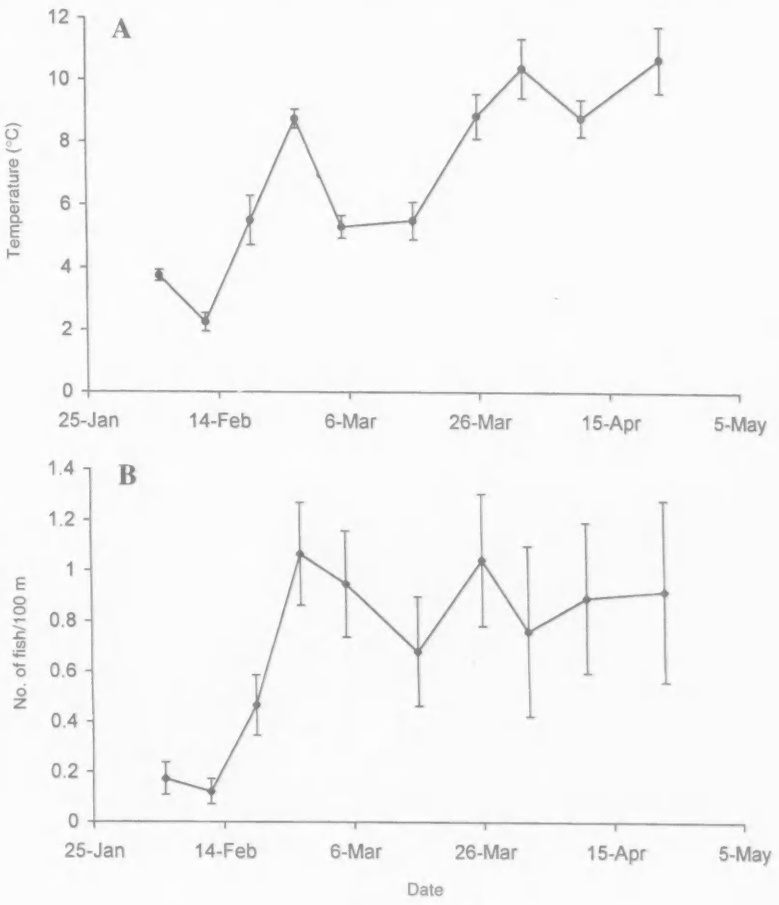

Figure 8

(A) Water temperature and **(B)** abundance of winter flounder in the Navesink River estuary during winter and spring 1997. Temperature values are means and ranges of temperature at the eight sampling stations. Values for flounder abundance are mean catch (±1 standard error) per 100-m distance over the bottom sampled by a 5-m otter trawl.

Discussion

Spawning behavior

Direct observation of spawning behavior has been documented for only a few flatfish, but spawning modes appear to vary substantially among species. Midwater pair-spawning has been observed in plaice (*P. platessus*; Forster, 1953), and in Dover sole (*Microstomus pacificus*; Baynes et al., 1994), but winter flounder spawned near the bottom and pairwise spawning (22%) was less common than spawnings involving multiple males (78%). Also, winter flounder spawning may be less elaborate or ritualized than in plaice or Dover sole or Caribbean bothids (Konstantinou and Shen, 1995). Although this could be an artifact of confinement, our research aquarium, with a bottom surface area of 46 m^2 and 3 m depth, was much larger than tanks where pair spawning has been observed in other species and where the density and size of fish were lower.

Our long-term observation of a single spawning population in the aquarium allowed us to record several different forms of reproductive behavior not reported earlier (Breder, 1922). Most notably, we were able to observe and record individual encounters

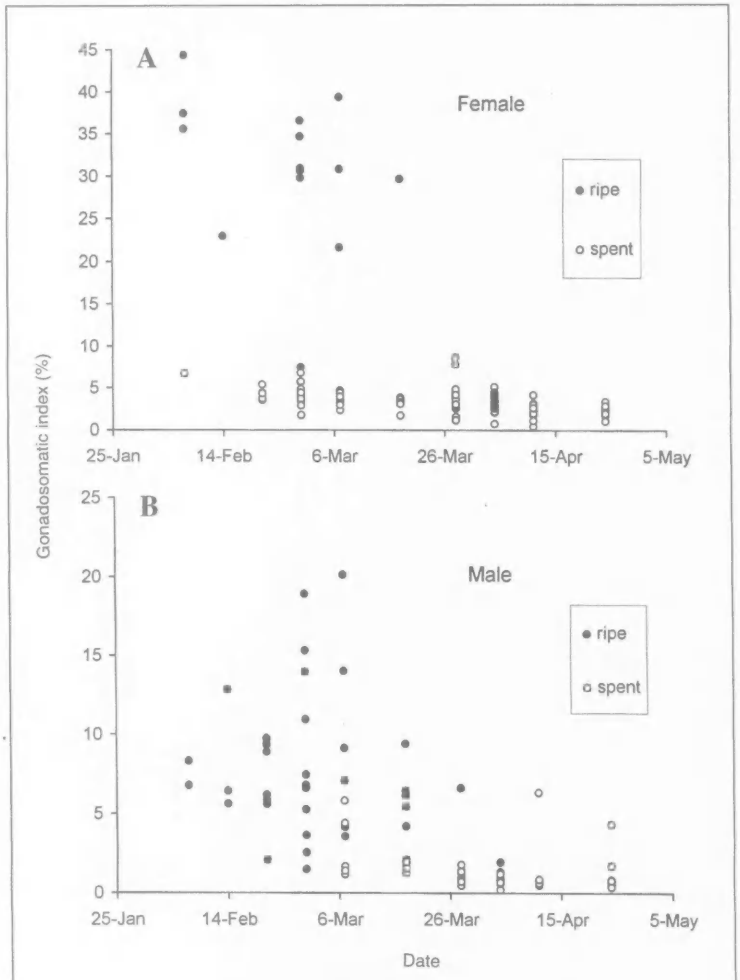

Figure 9

Gonadosomatic index (GSI) for winter flounder **(A)** females and **(B)** males shown as a function of collection date. The index was calculated according to LeCren (1951) as $GSI = 100(gonad\ weight/total\ body\ weight)$. Observational conclusions about the reproductive state of individual fish are shown by dots for ripe fish and circles for spent fish. Note the different *y*-axes.

between males and females. Unlike Breder, and in thousands of observed encounters, we never observed females initiating spawning activities. Breder acknowledged that his relatively small tanks may have altered normal behavioral patterns and was correct in predicting that males would be more active than females in a more open environment. In fact, males attempted to initiate spawning in the laboratory long before and after females were receptive. A similar phenomenon most likely occurs in the field, where males are ripe and capable of spawning for a longer period of time than females. Similarly, Rijnsdorp (1989) has observed that male plaice are in spawning condition for a period twice as long as that for females. As in our observations with winter flounder, Baynes et al. (1994) observed that males of *Microstomus* were much more active than females, and male attempts to initiate spawning were often rejected.

Male winter flounder were able to detect the presence of a spawning female from distances of at least 5–10 m in the research aquarium and frequently con-

verged suddenly on a spawning pair or group. A variety of sensory mechanisms could play a role in detecting opportunities for egg fertilization. Male fish may respond to the obvious visual signal of light reflected from the white underside of spawning fish. It is also possible that hydroacoustic cues were emitted from vigorous bouts of spawning that occurred just above the bottom. It is less likely that spawning was detected by an olfactory cue because there was almost instantaneous response to spawning activity and there was little horizontal current in the aquarium. However, olfactory cues may be important in certain circumstances. Occasionally, males converged on locations where spawning had occurred although the spawners had departed, and these spawning locations were sometimes visited by additional males for several minutes after the initial spawning event. Future research will be needed to determine the precise mechanisms of spawning group formation and detection.

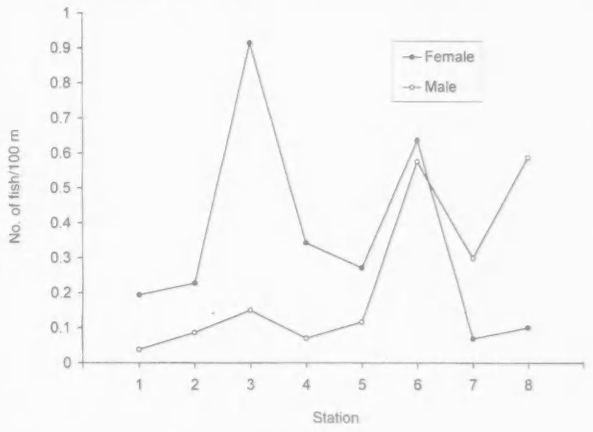

Figure 10

Mean catch by station number of male and female winter flounder per 100 m distance over the bottom in the Navesink River estuary. Values plotted are means for all dates combined.

In female winter flounder just one batch of oocytes matures per year (Burton and Idler, 1984); nevertheless, spawning in the aquarium population of winter flounder had a duration of 60 days. It is clear that individual females spawn many times over a period of at least one week, and perhaps longer. Circumstantial evidence indicates that individual males were capable of spawning over most of the reproductive season in the research aquarium. Large numbers of males were often engaged in single spawning events; the total number of spawnings yielded a high average spawning frequency by males that would necessitate several weeks of spawning by each; and feeding by males did not begin until most females stopped spawning. It is unknown whether male winter flounder produce more than one batch of sperm or simply release one batch over time (Bert et al., 1988).

Spawning in the aquarium occurred over a broad range of times, but always during hours of darkness or just before. Nocturnal spawning in winter flounder is probably a function of endogenous diurnal rhythms rather than light level because Breder (1922) noted that spawning occurred between 2200 and 0330 h even under artificial light. Spawning times vary with flatfish species and are probably species-specific. For example, plaice (Nichols, 1989) and other pleuronectids (Woodhead, 1966) are also known to spawn primarily at night, but *Bothus ocellatus* spawns only around the time of sunset (Konstantinou and Shen, 1995).

The role of multiple releases of eggs and sperm is poorly understood but may be important in the reproductive biology and recruitment of winter flounder. Although release of gametes could not be recorded or verified beyond the fact that larvae were produced in the aquarium, it is evident that numerous males spawned in response to one female. It is likely, therefore, that eggs released in a single spawning event were often fertilized by more than one male. Given that the average female fish spawned 40 times during the reproductive season in the aquarium and that most of the males appeared to remain ripe throughout the observation period, it is likely that many, if not all, of the males could have contributed genetic material to the offspring of each female. Genetic diversity of embryos produced in the field could be high for similar reasons.

Although male winter flounder appeared to be in a constant state of readiness for spawning, future experiments will be needed to determine whether frequency of spawning and fertilization success is uniform among individuals and how this might be influenced by size structure, sex ratio, or density of fish on the spawning ground. For example, small (10–15 cm) but reproductively ripe males were abundant in the Navesink River estuary. It is possible that these small individuals have a lower frequency of success than large males in inducing females to spawn, given the order-of-magnitude difference in body weight between 10 and 22 cm fish. However, Baynes et al. (1994) observed female Dover sole spawning with males smaller than themselves, and

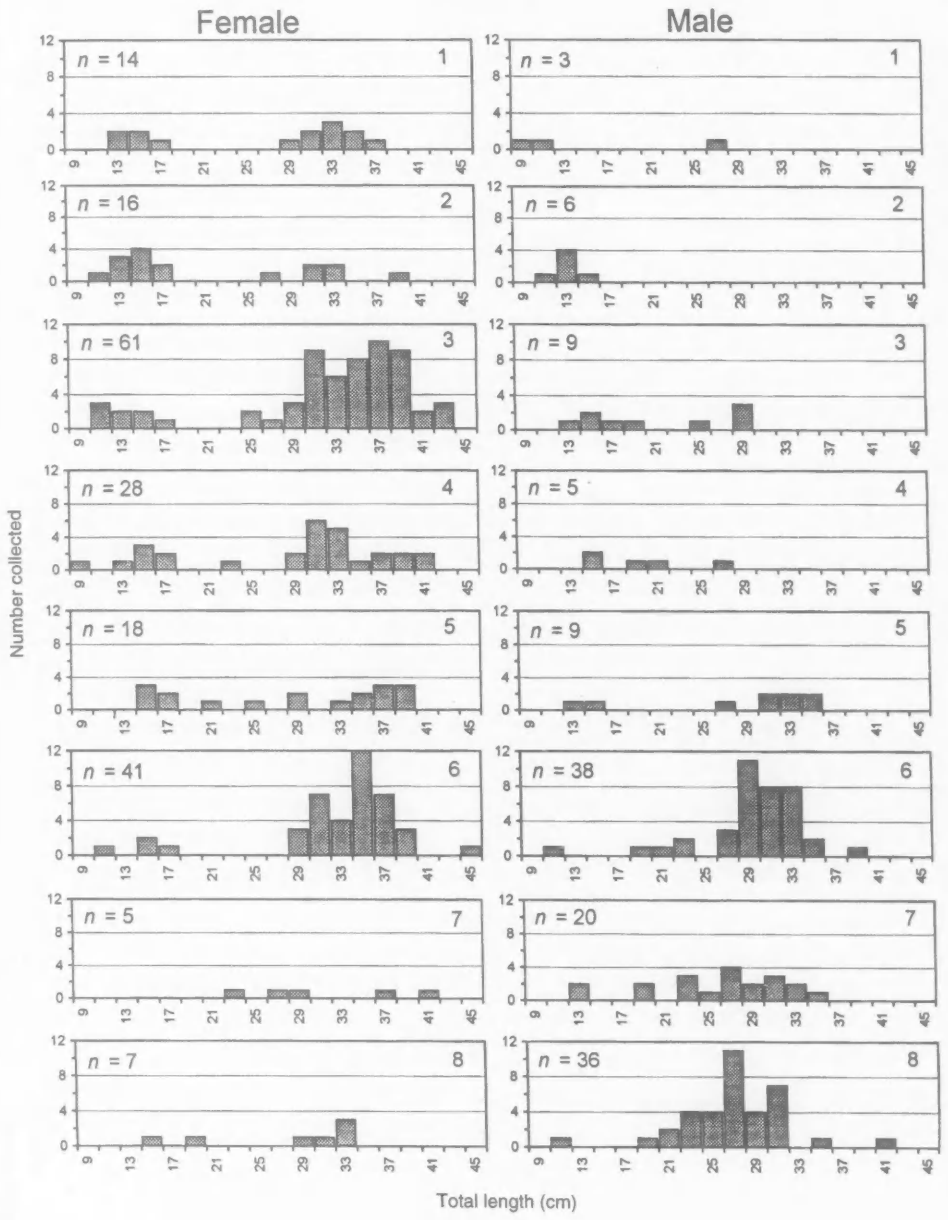

Figure 11

Length-frequency distributions for female and male winter flounder in the Navesink River estuary, plotted by field station.

the same may occur with winter flounder. On the other hand, most fertilization by small males may occur during group spawning. "Sneaking," whereby subordinate males approach and fertilize some of the eggs when a pair is spawning, is a reproductive behavior common in a variety of fishes (Chan and Ribbink, 1990; Oliviera and Almada, 1998). We observed no overt agonistic behavior in our long-term experiment, and there is no reason to believe that small males do not contribute to the reproductive population.

Spawning, migration, and habitat use

Previous studies have shown that winter flounder in the mid-Atlantic region migrate to shallow inshore waters to spawn during the late winter (Perlmutter, 1947; Poole, 1966; Scarlett and Allen, 1992), and it is known that the Navesink-Shrewsbury River estuarine system is an important spawning ground (Phelan, 1992; Scarlett[1]). Phelan's study and our investigation provide direct evidence that winter flounder immigrate to the Navesink estuary between early February and March. Flounder abundance was lowest when water temperature was lowest (2.2°C in mid-February) and increased rapidly with subsequent temperature rise. In fact, high and relatively constant catches of winter flounder occurred in the Navesink estuary at temperatures of 6–11°C. This is consistent with earlier observations that adult winter flounder emigrated from bays in southern New Jersey when water temperature declined below 3.5°C and returned when temperature rose to 6°C (Danila, 1978). Most adult males and females had ripe gonads upon entry to the system in late winter, and most were spent by the end of April. This pattern of seasonality is consistent with previous findings (Pearcy, 1962; Scarlett and Allen, 1992).

It is likely that the most important spawning area for winter flounder in the Navesink River was in the middle reach. Reproductively ripe male winter flounder were found throughout the estuary; however, highest numbers of ripe females were found west of station 5, and only one nearly spent female was collected farther down the estuary. Scarlett and Allen (1992) found that the middle reach of the Manasquan River estuary, New Jersey, was a major spawning ground for winter flounder, as were the upper reaches of the Mystic River estuary, Connecticut (Pearcy, 1962), and Narragansett Bay, Rhode Island (Powell[2]).

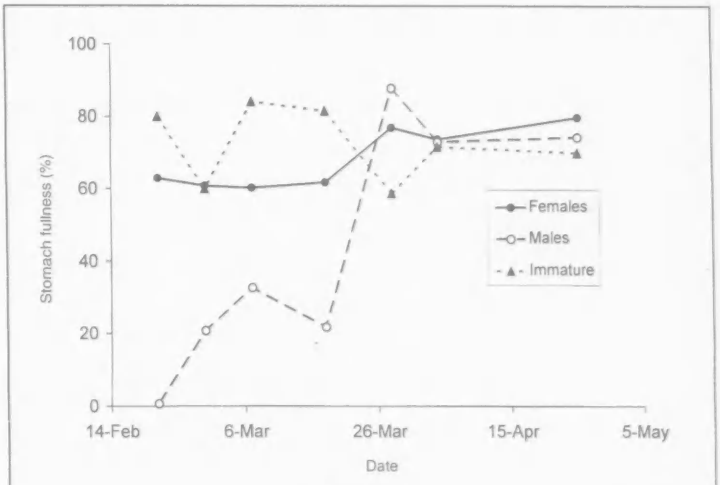

Figure 12

Temporal variation in percent stomach fullness of winter flounder in the Navesink River estuary. Fullness indices are shown by adult gender and for immature fish.

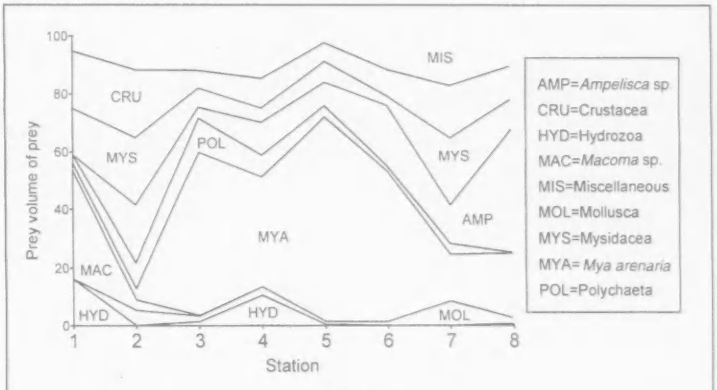

Figure 13

Composition of diet by percentage volume in winter flounder collected at eight stations along the length of the Navesink River estuary during winter and spring 1997.

Several different physical and chemical factors could affect the location of spawning habitats. Temperature may have influenced the seasonal migration to the Navesink estuary; however, there was little variation in temperature along the axis of the estuary, and other factors probably influenced exact spawning location. McCracken (1963) found that adult winter flounder died in 8 ppt salinity; therefore, upstream migration is probably limited by this variable. Neither males nor females were abundant in locations where salinity was frequently near or below 10 ppt.

[2] Powell, J. C. 1989. Winter flounder tagging study, 1986–1988, with comments on movements. Rhode Island Division of Fish, Wildlife, and Estuarine Research, P.O. Box 218, West Kingston, Rhode Island 02892. Unpubl. report.

The location of spawning in an estuary may also be related to temperature and salinity requirements of the demersal eggs. Scarlett and Allen (1992) collected eggs at salinities of 14–32 ppt and temperatures of 0.9–10°C in the Manasquan estuary, about 30 km south of our study site. Rogers (1976) found that the highest proportion of viable hatches occurred at 3°C over a salinity range of 15–35 ppt. At temperatures over 3°C, the optimal range was 15–25 ppt, which closely matches temperature and salinity ranges in the middle reach of the Navesink River.

Other factors that may influence the choice of spawning habitat by winter flounder are hydrodynamic properties and associated sediment characteristics. Strong flood tidal currents that characterize the lower Navesink River attenuate rapidly in the middle reach (Chant[3]). This attenuation is associated with deepening of the estuary and general reduction of sand bars, decrease in the mean grain size of sediments, and increase in sediment organic content (Stoner, unpubl. data). It is unknown whether spawning winter flounder respond to any of these habitat characteristics; however, the depositional qualities of the upper estuary and flood-dominated circulation may aid in the retention of winter flounder eggs and the evolution of habitat choice in spawners. Crawford and Carey (1985) noted that winter flounder spawned in two sites in an estuarine lagoon in Rhode Island where hydrodynamic features retained larvae. It is plausible that habitat choice, cued by either fine-grained sediments or low current velocities, could be associated with such retention features.

Seasonal variation in feeding activity

The general conclusion has been that winter flounder are opportunistic feeders, consuming polychaetes, small crustaceans, molluscs, and other prey according to their abundance (Pearcy, 1962; Richards, 1963; Klein-MacPhee, 1978; Franz and Tancredi, 1992; Martell and McClelland, 1994; Steimle et al., 1994; Carlson et al., 1997). Winter flounder collected in the Navesink River during this investigation consumed a mixture of invertebrate prey, but the vast majority of the diet was siphons of the soft clam *Mya arenaria*. The abundance of spent and feeding flounder in the lower estuary may, in fact, be associated with the observed abundance of this preferred prey in that location.

Cessation of feeding by adult winter flounder during the winter has been noted previously (Tyler, 1972; Martell and McClelland, 1994), but we found that feeding was influenced strongly by gender and reproductive state. Both in the field and in the aquarium, female flounder appeared to resume feeding immediately after they completed spawning for the season. Early feeding probably provides an advantage for female fish because ovarian development for the next spawning season begins immediately after spawning (Burton and Idler, 1984). In the field, males did not begin feeding until the end of March, and feeding in the aquarium was light until after the last spawning events. We conclude that male behavior is dedicated to fertilizing the maximum number of eggs, at the expense of feeding and late winter growth.

There is now substantial evidence for seasonal variation in daily activity and feeding rhythms in winter flounder. During the summer, winter flounder are primarily diurnal in general activity (Olla et al., 1969) and feeding (MacDonald and Waiwood, 1987). Bharadwaj (1988) found that adults fed throughout the day and night in November, speculating that this was related to maturation of gonads for the winter spawning season. In our aquarium observations, adult winter flounder were almost entirely nocturnal throughout the spawning season, remaining buried during the day. Daytime activity began again when spawning was completed and increased throughout the remainder of the postspawning period. Primarily daytime activity during the nonspawning season could be associated with visual predation modes (Olla et al., 1969), but it remains to be determined how mates are located in darkness and why spawning occurs at night.

Conclusions

This study provides the first detailed observations on winter flounder spawning since Breder's (1922) original description over 75 years ago, and the combination of laboratory and field work provides new insight into the biology and ecology of spawners. The behavior of male winter flounder appears adapted to maximize encounters with reproductive females and numbers of eggs fertilized. From our field collections, it is apparent that one-year-old male winter flounder (10 cm TL) are capable of spawning, whereas female spawners all appeared to be at least two years old. Males also became reproductively ripe earlier in the season than did females and remained ripe to a later date than most females. Males were more active than females, had higher swimming speeds, and initiated all spawning events. The males fed very little during the reproductive season and appeared

[3] Chant, R. J. 1998. Institute of Marine and Coastal Sciences, Rutgers University, P.O. Box 231, New Brunswick, New Jersey 08903. Unpubl. data.

to sacrifice winter growth to maintain a high level of reproductive behavior.

Spawning frequency was high in both males and females. Individual females were capable of spawning as many as 40 times over a period of at least one week, and males spawned throughout the season (at a rate at least three times the female rate) and perhaps several times per day. Clearly, individual records of spawning behavior would be useful in understanding the reproductive role of one-year-old males and in determining the duration of spawning in individual females. Given the frequency of spawning in both male and female winter flounder and the fact that several males may release sperm in response to egg-laying by one female, we conclude that the genetic diversity of offspring produced by a female in one year is probably very high.

Although our data provide new insights into the natural history and reproductive behavior of winter flounder, several questions important to sound management of spawning stocks remain to be answered. For example, we do not know if reproductive populations are scattered in estuarine and coastal waters or are concentrated in spawning aggregations on specific spawning grounds. We saw a concentration of ripe fish in the middle reach of the Navesink River estuary, but ripe fish were also present in a variety of habitats in adjacent Raritan Bay during the winters of 1997 and 1998 (Stoner and coauthors, personal obs.), and it is possible that winter flounder spawn in more than one location over the spawning season. It is also important to learn whether or not spawning behavior and reproductive output from a spawning ground are density-dependent.

Acknowledgments

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Population size of humpback whale, *Megaptera novaeangliae*, in waters off the Pacific coast of Mexico

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Abstract.—The humpback whale (*Megaptera novaeangliae*) is a cosmopolitan species whose stocks were drastically decreased by commercial whaling practices prior to 1967. The North Pacific population was estimated to be between 15,000 and 20,000 animals before the practice of whaling. At the time of the commencement of its international protection in 1967, this population may have been reduced to fewer than 1000 individuals. The Pacific coast of Mexico and the Revillagigedo Archipelago constitute one of the main breeding and calving areas for North Pacific humpback whales. The objective of this paper is to present an estimation of abundance of humpback whales in this region based on photographic identification of individual animals. Estimates of population size were obtained by using mark and recapture models for both closed and open populations, with each year representing a capture occasion. A total of 1184 humpback whales were identified in Mexican waters between 1986 and 1993. The best estimates of population size for the Mexican stocks were those provided by the modified Jolly-Seber method: 1813 (95% CI: 918–2505) for the coastal stock in 1992, and 914 (95% CI: 590–1193) for the Revillagigedo stock in 1991.

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Fish. Bull. 97:1017–1024 (1999).

Humpback whales, *Megaptera novaeangliae*, make seasonal migrations between low-latitude wintering areas used for mating and calving and high-latitude feeding areas. The general distribution of feeding areas in the North Pacific covers coastal waters in the western North Pacific from northern Japan throughout the Bering Sea and in the eastern North Pacific as far south as southern California. During the winter breeding season, these whales congregate in three geographically isolated tropical areas: the Ryukyuan, Bonin, and Mariana Islands south of Japan; the islands of the Hawaiian Archipelago; and the Pacific coast of Mexico and the Revillagigedo Archipelago (Rice, 1974; Johnson and Wolman, 1984).

Humpback whales have been listed as endangered since severe reduction of all stocks worldwide by commercial exploitation (Rice, 1974; Gambel, 1976). The number of these whales were estimated to be between 15,000 and 20,000 animals before whaling depleted them during the first half of the 20th century; at the time of its international protection in 1967 this population may have been reduced to fewer than 1000 individuals (Rice, 1974, 1978). However, the reliability of these figures is unknown.

The extent of the recovery in the North Pacific population over the last 25 years is debatable. Estimates of abundance with mark and recapture techniques based upon photo-identification data have been made for different areas of this ocean, but there has been much debate regarding the reliability of such estimates (Darling et al., 1983; Baker et al., 1986; Darling and Morowitz, 1986; Baker and Herman, 1987; Alvarez et al., 1990; Calambokidis et al., 1990; Cerchio, 1998; Calambokidis et al.[1]). There is currently insufficient evidence to assess whether a significant change in abundance has occurred since whaling ceased.

Three main wintering aggregations of humpback whales are recognized off the Pacific coast of Mexico: the Baja California Peninsula; the mainland coast of Mexico (including, Isabel Island, Tres Marias Islands, and the mainland coast); and the Revillagigedo Archipelago (including Socorro, San Benedicto, Roca Partida, and Clarion Islands) (Rice, 1979; Urbán y Aguayo, 1987).

The comparison of photo-identified humpback whales in these wintering grounds showed that there was a greater affinity between whales off Baja California and those off the mainland coast of Mexico than those off either Baja California or the mainland coast and those off the Revillagigedo Archipelago (Urbán et al., 1989; Ladrón de Guevara et al., 1993; Jaramillo, 1995) (Table 1). From these results, two different population units of humpback whales during winter in Mexican waters were previously proposed: the coastal Stock (including Baja California and mainland coast of Mexico), and the Revillagigedo stock (Alvarez et al., 1990; Urbán et al.[2]) (Fig. 1).

Table 1

Matches (above the diagonal) and interchange index[1] (below the diagonal) among the three main wintering aggregations in the Mexican Pacific. Sample size in parentheses.

	Baja California Peninsula (471)	Mainland coast of Mexico (383)	Revillagigedo Archipelago (450)
Baja California Peninsula	—	64	20
Mainland coast of Mexico	0.38	—	23
Revillagigedo Archipelago	0.12	0.18	—

[1] Index of interchange.
This index quantify the degree of interchange among two samples (among regions) that accounted for sample size:

$$Index\ of\ interchange = (m_{12}/(n_1 \times n_2)) \times 1000,$$

where n_1 = whales identified (captured) in sample 1;
n_2 = whales identified in sample 2; and
m_2 = captured whales from sample 1 recaptured in sample 2.

(see Baker et al. 1985; Cerchio et al., 1998).

This division of winter aggregations is also supported by mitochondrial DNA lineage analyses (Medrano-Gonzalez et al., 1994, 1995a, 1995b); however, because the waters off California, Oregon and Washington are the primary feeding destination of the whales observed in Baja California and the mainland coast, the migratory destination of the whales seen around the Revillagigedo Islands is still unknown (Urbán et al. 1987; Urbán et al.[3]).

Previous estimates of humpback whale abundance in Mexican waters are the following: 500–600 for Socorro Is. (Campos, 1987); 200–400 for Isabel Is. (Alvarez, 1987); 600–700 for the mainland coast (Alvarez et al., 1990); and 1200–1700 for all the Mexican Pacific (Urbán et al., 1989). However, it is recognized that these estimates were based on limited data and on assumptions that generally were not tested.

In our study we present an analysis of photographic data obtained during the winter breeding and calving seasons from 1983 to 1993 in the different assembly areas of the Mexican Pacific. We use this analysis to calculate reliable independent estimates of abundance of humpback whales for the coastal and the Revillagigedo stocks.

[1] Calambokidis, J., G. H. Steiger, J. Straley, T. J. Quinn II, L. M. Herman, S. Cerchio, D. Salden, M. Yagamuchi, F. Sato, J. Urbán R., J. K. Jacobsen, O. von Ziegesar, K. C. Balcomb, C. M. Gabriele, M. E. Dahlheim, N. Higashi, S. Uchida, J. K. B. Ford, Y. Miyamura, P. Ladrón de Guevara P., S. A. Mizroch, L. Shlender, K. Rasmussen. 1977. Abundance and population structure of humpback whales in the North Pacific basin. Final Rep. to Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, La Jolla, CA, 72 p.

[2] Urbán R., J., J. C. Salinas V., A. Guillén G., and E. Vázquez M. 1997. La ballena jorobada *Megaptera novaeangliae* en al Península de Baja California Sur, México. Final Report to the Biodiversity National Commission (CONABIO). Contract H035, 41 p.

[3] Urbán R., J., A. Jaramillo L., A. Aguayo L., Paloma Ladrón de Guevara P., M. Salinas Z., C. Alvarez F., L. Medrano G., J. Jacobsen, K. C. Balcomb, D. E. Claridge, J. Calambokidis, G. H. Steiger, J. M. Straley, O von Ziegesar, S. Mizroch, .M. Dahlheim, J. M. Waite, J. D. Darling, and C. S. Baker. 19xx. Migratory destination of the Mexican Pacific humpback whales. Universidad Autónoma de Baja California Sur, Ap. Post. 19-B, La Paz, Baja California Sur, Mexico.

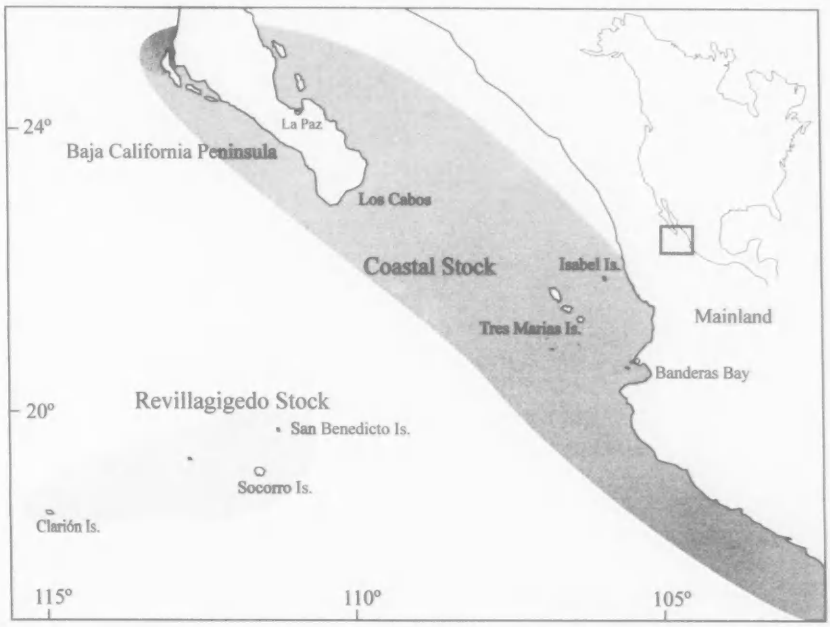

Figure 1

Study area showing, by shading, the distribution of the Revillagigedo and coastal stocks.

Materials and methods

Individual identification

Humpback whales were individually identified from photographs taken by different institutions from approximately December to March, along the mainland coast of Mexico (1983–92), from mid-January to March in Baja California (1987–93), and at the Revillagigedo Archipelago (1986–92) (Table 2).

Although photo-identification data have been available for the coastal stock since 1983 and for the Revillagigedo stock since 1985, efforts before 1986 were limited in time and space, and also lacked continuity. Beginning in 1986, surveys were conducted off Socorro Island for the Revillagigedo stock, and near San José del Cabo or the mainland coast (or both) for the coastal stock. No data were obtained for either Revillagigedo or the mainland in 1993.

The whales were identified individually through photographs of the black and white pigmentation patterns on the ventral surface of their flukes (see Katona and Whitehead, 1981). Photographs were obtained with 35-mm cameras equipped with 200–300 mm lenses. Although the film used varied by region and season, most photographs were taken with black and white Kodak Tmax 400 ISO pushed to 1600 ISO, ensuring shutter speeds as high as 1/1000 of a second.

On the basis of focus, angle, and light conditions, all fluke photographs were judged to be either good, fair, or of poor quality; only photos in the first two categories were included in this study. Within these quality levels, the whales showed at least 50% of each fluke at a sufficiently vertical angle to allow the shape of the trailing edge to be distinguished. Calves were excluded from the analysis owing to their tendency to show changes in pigmentation patterns during the first year of life (Carlson et al., 1990). Selected photographs were compared visually by at least three persons with experience in matching humpback whales flukes photographs from both Universidad Nacional Autonoma de Mexico and Universidad Autonoma de Baja California Sur.

Abundance estimation

Abundance estimates were obtained by using an eight-year period for the coastal stock, from 1986 to 1993, and a seven-year period for the Revillagigedo stock, from 1986 to 1992.

Estimates of population size were obtained by using mark and recapture models for both closed and open populations, with each year representing a capture occasion. The time span of the study was seven years; consequently, although calves were not included in the analysis, it is inevitable that additions

Table 2

Study periods and data sources for each of the regions. UNAM = Universidad Nacional Autonoma de Mexico; UABCS = Universidad Autonoma de Baja California Sur; CWR = Center for Whale Research; CS =Cousteau Society.

Region	Season	Study period	Source
	1986	20 Dec 85–4 Mar 86	UNAM
	1987	25 Dec 86–20 Mar 87	UNAM
	1988	22 Jan 88–8 Feb 88	UNAM
	1989	24 Jan 89–5 Mar 89	UNAM
	1990	25 Nov 89–21 Mar 90	CWR, UABCS, UNAM
	1991	28 Nov 90–26 Feb 91	UNAM
	1992	26 Dec 91–6 Mar 92	UNAM
Baja California Peninsula	1987	10 Feb 87–5 Mar 87	CWR, UABCS
	1988	6 Feb 88– 8 Mar 88	CWR, UABCS
	1989	23 Jan 89–25 Mar 89	CWR, UABCS
	1990	20 Feb 90–31 Mar 90	CWR, UABCS
	1991	24 Jan 91–23 Mar 91	UABCS
	1992	20 Jan 92–2 Apr 92	UABCS
	1993	15 Jan 93–5 Apr 93	UABCS
Revillagigedo Archipelago	1986	16 Jan 86–20 Feb 86	UNAM
	1987	20 Jan 87–5 Mar 87	UNAM
	1988	1 Feb 88–9 Mar 88	UNAM
	1989	16 Jan 89–7 Mar 89	UNAM
	1990	31 Jan 90–20 Mar 90	UNAM
	1991	15 Jan 91–25 Apr 91	UNAM
	1992	25 Apr 92–7 May 92	UNAM, UABCS, CS

to the population were occurring in the form of animals born in previous years that became identifiable as they grew. Also, some individuals died. Because we would therefore expect to be studying an open population, we chose the Jolly-Seber mark and recapture model. One of the critical assumptions of this method is the highly unlikely condition that all animals have the same capture probabilities at the moment of the sample (Seber, 1982). If heterogeneity in capture probabilities is present, the open population models will underestimate population size to a greater extent than closed population models (Carothers, 1973; Pollock et al., 1990). Given that there was no way to account for such problems with open population models (Hammond, 1986), we decided to use closed population models to test for variations in capture probabilities.

Closed population estimates were obtained and assumptions were tested by using the software program CAPTURE developed by Otis et al. (1978), which included an algorithm to select the appropriate model after the hypothesis testing procedure. The conceptual basis for this selection procedure is a tradeoff between precision and bias. If a simple model, such as the null model M_0 in Otis et al. (1978), is used to estimate parameters from data that violates in any way the assumption of equal capture probability, then significant biases are introduced in parameter estimates and sampling variances will be artificially small. On the other hand, if a more complex model is used, such as M_{th} of Otis et al.. (1978), that allows capture probabilities to vary with time and among individuals, biases may be reduced but the sampling variance will be greater than it should be. The selection procedure takes into account the individual goodness-of-fit tests performed for specific models on the data and the confrontation of related models (i.e. where one model is a particular case of a general one). The significance levels for all these tests are combined in a standard discriminant analysis and the resulting statistic is standardized so that its value ranges from 0 to 1, 1 being the score that indicates the appropriate model (Otis et al., 1978).

The basic or null model M_0 can be applied to the general case of multiple recaptures in a closed population, where all animals have equal capture probabilities, and where this probability remains constant in time. The model that allows the capture probability to vary in time, simultaneously permitting individuals to have unequal capture probability (Chao et al., 1991: model M_{th} in Otis et al., 1978) was selected for estimation of both stock sizes. In addition,

abundance was also estimated for the coastal stock by using the model that only allows relaxation of the requirement for constant capture probability in time (Darroch, 1958: model M_t in Otis et al., 1978). Model M_{th} provides the estimator of population size for a situation where capture probabilities vary in time and among individuals. Model M_t provides the estimate of population size when capture probabilities are the same among individuals but vary in time (Otis et al., 1978).

Outputs from CAPTURE were used only as a "screening technique," as suggested by Menkins and Anderson (1988) to investigate departures from the assumption of equal catchability. The test for population closure within CAPTURE was ignored because its power is low (Otis et al., 1978).

Open population estimation was done through the software program RECAP[4] This program provides estimates of parameters under the basic Jolly-Seber model where all individuals have equal capture probabilities and survivorship, but these were allowed to vary between sampling occasions. Also, it incorporates a modification of the Jolly-Seber model (modified J-S model) that constrains estimates to feasible values, stabilizing them and providing more reliable confidence intervals (Buckland, 1980). Open population estimates were also obtained by using the software program JOLLY described by Pollock et al. (1990). Of particular interest is the goodness-of-fit tests performed for this program to investigate how well our data are explained by the Jolly-Seber model or any of the variants included in the program. The results obtained under such variants were also very useful because they allowed for the estimation of more precise parameters when either capture probabilities or survivorship (or both) were kept constant. Even in the case when the more general Jolly-Seber model was chosen (model A), observation of survivorship estimates under model 2 (temporary trap response model) were useful to look for the amount of transit within the areas occupied by each stock.

Table 3

Number of humpback whales identified in Mexican waters from 1986 to 1993.

Region	1986	1987	1988	1989	1990	1991	1992	1993
Coast								
Animals caught	74	71	74	83	218	109	180	92
Newly caught	74	65	61	67	174	91	140	61
Revillagigedo								
Animals caught	26	41	73	106	48	189	36	
Newly caught	26	37	64	86	33	143	23	

Table 4

Estimates of population size (N) with closed population models (see "Materials and methods" section for descriptions of the models).

Model	N	95% CI	Capture prob. P
Coastal stock			
M_o	2039	1728–2194	0.05
M_t[1]	1828	1660–2076	0.06 average
M_{th}[1]	2188	1861–2612	0.05 average
Revillagigedo stock			
M_o	1078	807–1169	0.0687
M_t	874	762–1020	0.084 average
M_{th}[1]	1308	1043–1684	0.057 average

[1] Selected models.

Results and discussion

Photo identification

A total of 1184 humpback whales were identified in Mexican waters between 1986 and 1993. Of the total, 733 individuals were observed in the area occupied by the coastal stock, 412 in Revillagigedo, and 39 in both areas (a summary of the number of individuals identified in each area is provided in Table 3).

Abundance estimation

The closed population estimators showed that heterogeneity and variations in capture probabilities in time are present in both stocks. However, the confidence intervals built for models M_t and M_{th} overlap to a greater extent in the coastal estimates than in the Revillagigedo estimates, indicating that both models M_{th} and M_t are equally good for the coastal stock (Table 4). These relatively small capture probabilities estimated with the closed models are consistent with a positive bias in the population size estimates because, as will be discussed, the populations were open through the period of study. Therefore, the closed population models were useful in showing that the assumption of equal catchability is not met.

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Table 5

Estimates of population size (N) with the program JOLLY, model A (general) (see "Materials and methods" section for descriptions of the models).

Year	N	95% CI	Capture prob. P
Coastal stock[1]			
1987	771	119–1424	0.08
1988	484	215–753	0.14
1989	791	382–1220	0.10
1990	1247	682–1811	0.17
1991	1660	610–2712	0.06
1992	1702	488–2917	0.10
Average	1109	793–1425	0.11
Revillagigedo stock[2]			
1987	134	13–256	0.25
1988	367	125–609	0.18
1989	593	288–897	0.17
1990	456	179–733	0.10
1991	1569	−140–3277	0.12
Average	623	268–980	0.16

[1] χ^2 Goodness-of-fit model A $x = 5.968$ $P = 0.8754$
χ^2 Goodness-of-fit model 2 $x = 1.132$ $P = 0.8892$
[2] χ^2 Goodness-of-fit model A $x = 13.23$ $P = 0.0667$
χ^2 Goodness-of-fit model 2 $x = 0.448$ $P = 0.799$

Table 6

Estimates of population size (N) with the program RECAP, modified Jolly-Seber model (see "Materials and methods" section for descriptions of the models).

Year	N	95% CI	Capture prob. P
Coastal stock			
1987	822	425–1142	0.09
1988	580	327–931	0.13
1989	825	519–1229	0.10
1990	1120	824–1613	0.19
1991	1813	1168–2686	0.06
1992	1813	918–2505	0.10
Average	1162	889–1406	
Revillagigedo stock			
1987	167	49–484	0.25
1988	414	215–691	0.18
1989	610	388–825	0.17
1990	606	359–891	0.08
1991	914	590–1193	0.21
Average	642	373–677	

The Jolly-Seber analysis indicated that the open population model explained in a better way the data for both Revillagigedo and coastal stocks (Table 5). In the Revillagigedo stock the goodness of fit χ^2 test on model A (general model) did not reject the null hypothesis (P=0.0667), but the result showed that data are better explained (P=0.799) by model 2 (temporary trap response model), assuming that survival rates of newly captured animals differ from those of previously captured animals. In other words, this test indicates that some animals may have moved into the capture site and once captured, they could have left and even re-entered the sampling area. This inference an be supported by the fact that data for this stock were collected only in Socorro Island and that some animals may have a preference for anther island, such as Clarion, far away from the sampling area (Fig. 1). For the coastal stock, the goodness-of-fit χ^2 tests indicate that the model A (P=0.8754) and model 2 (P=0.8892) are almost equally good in explaining the data. Although sampling coverage was wider for this stock, allowing a better collection of photographs for moving animals, this problem still remained, but had a smaller effect on the estimates.

Having accepted that the Jolly-Seber model explained the data well for the two stocks, population-size estimates were obtained with the software program RECAP. Results show that the modified estimator (modified J-S model) provided more stable estimates and narrower and more realistic confidence intervals (Table 6).

Because capture probabilities are larger than those obtained by the closed population methods, and considering that the Jolly-Seber estimates may be negatively biased given heterogeneity, population size are likely overestimated by the closed population methods.

In light of the above arguments, we conclude that the best estimates of population size for the Mexican stocks, using the data at hand, are those provided by the modified Jolly-Seber model of program RECAP. Estimates obtained with closed population methods are not recommended when data are pooled for the whole extension of the study; however, it may be worth obtaining estimates with pairs of years with models testing for heterogeneity and capture probabilities varying with time, although certain information and precision may be sacrificed.

Estimates for each year show an apparent trend towards increase for both stocks. Such a trend was considered an artifact of a reduction in the bias caused by heterogeneity in capture probabilities after sample size increased with time. Consequently, we consider that the best estimates for the stock sizes were those obtained for the last years and are 1813 (95% CI: 918–2505) for the coastal stock in 1992, and 914 (95% CI: 590–1193) for the Revillagigedo stock in 1991.

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Extraordinary abundance of squid paralarvae in the tropical eastern Pacific Ocean during El Niño of 1987

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Abstract.—A two-ship survey of the eastern tropical Pacific collected surface plankton samples during El Niño in August–November 1987. Although the diversity of cephalopods in these samples was low, cephalopod abundance was extremely high. Most of the cephalopods collected were rhynchoteuthion paralarvae of an ommastrephid squid, either *Doscidicus gigas* or *Sthenoteuthis oualaniensis*. High abundances (hundreds of paralarvae in a 15-min tow) were concentrated in a band parallel to the coast, 740–900 km off Central America. This band of high abundance was approximately coincident with the 29°C surface isotherm. Maximum abundance (>12,000 rhynchoteuthions in a 15-min tow) was four orders of magnitude greater than background levels and an order of magnitude greater than any other report of cephalopod abundance. Based on flowmeter readings from the sampler, the anomalous abundance was not a sampling artifact. Size-frequency analysis indicates that this patch cannot be explained as a result of recent hatching from an egg mass. This abundance may have resulted from warm El Niño waters, aggregation by convergence of surface currents, or the interaction of these factors during the squid's spawning season.

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Reports of the effects of El Niño/Southern Oscillation have been widespread in both scientific literature and popular news media. Shifts in distribution and decreases in abundance of marine animals resulting from El Niño have received much attention. Cephalopods are important components of the marine food web, as well as the targets of commercial fisheries. I report here on the serendipitous collection of squid paralarvae during El Niño 1987 at abundances an order of magnitude higher than any previously known.

Materials and methods

A two-ship survey for a visual census of marine mammals was conducted in the eastern tropical Pacific Ocean during August–November 1987. During four cruise legs, the NOAA Ship *David Starr Jordan* surveyed the area between the equator—19°N and 79–121°W, while the NOAA Ship *MacArthur*, also in four legs, covered the region westward of the *Jordan* survey to 148°W and southward to 11°S. Surface plankton samplers (Manta nets; Brown and Cheng, 1981) were towed by both ships almost every day after sunset to collect fish larvae. Surface temperature was measured by bucket thermometer concurrently with each plankton tow. The distance of each tow was estimated by a flow meter mounted below the net. Extremely high numbers of cephalopod paralarvae were found in some of these samples when they were sorted for ichthyoplankton after the conclusion of the cruises.

Results

The diversity of cephalopods in these samples was quite low; only 15 species were identified and >99% of the 15,052 cephalopods collected were a single species of the squid family Ommastrephidae (Table 1). Ommastrephid paralarvae are distinctive and are referred to as rhynchoteuthions because the two tentacles (as opposed to the eight arms) are fused throughout the early life history. Throughout the entire surveyed region, abundance of paralarval ommastrephids, measured as number of rhynchoteuthions collected per 15-min tow, generally was 0–10 squids per tow. Maximum abundance (22 stations with 20–>100 rhynchoteuthions/tow) was found about 740–900 km offshore in a band parallel to the coast of Central America (Fig. 1A). Within this band at three stations during two separate legs, 379, 461, and 12,354 rhynchoteuthions were collected, respectively. Although most of the stations in this band were sampled by the *Jordan*, the northeasternmost *MacArthur* stations were in the eastern end of

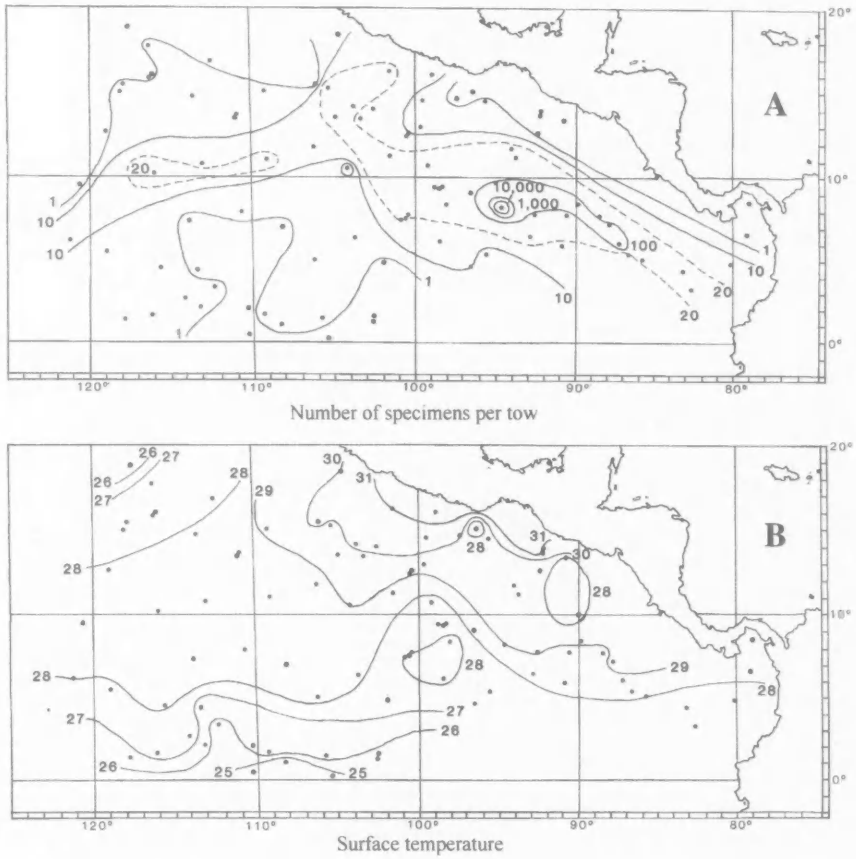

Figure 1

NOAA Ship *D.S. Jordan* cruise 8710, August–November 1987: (**A**) sampling locations and isolines of abundance for rhynchoteuthion squid paralarvae; (**B**) surface isotherms (°C).

the band. A secondary patch of abundance (five stations with 20–90 rhynchoteuthions/tow) was sampled by the *MacArthur* farther to the west (9–13°N, 121–135°W) and appeared to be a westward extension of the band of peak abundance.

The primary band of maximum abundance was approximately coincident with the 29°C surface isotherm (Fig. 1B). Peak abundance was found in the vicinity of a very productive oceanographic upwelling feature known as the Costa Rica Dome (Li et al., 1983). The secondary patch of abundance was in an area with surface temperatures in the mid-28°C range. It may be associated with a westward extension of the Costa Rica Dome, termed the countercurrent ridge (Fiedler et al., 1991). A plot of abundance versus surface temperature shows a clear peak between 27.5° and 31.0°C (Fig. 2). The three stations with highest abundances were all in areas of 29.0–29.5°C surface temperatures (see vertical arrows in Fig. 2). Abundance tapered off late in the survey although surface temperatures remained above 27.5°C (Fig. 3), within the optimum range indicated by peak abundance.

In addition to a biological-oceanographic pattern of abundance, two other alternatives could explain the pattern described here: 1) it could represent concentrated patches of recent hatchlings from isolated egg masses; or 2) it could result from sampling error associated with changes in towing characteristics of the samplers (e.g. speed, duration).

To address alternative 1, I examined size-frequency distributions based on dorsal mantle lengths (DML), both within individual samples and in the total pooled population. For samples with >100 specimens, I measured a subsample of 100. I separated the stations into dusk tows (within one hour after local sun-

Table 1

Cephalopods collected by Manta-net surface zooplankton samples during the two-ship survey of the eastern tropical Pacific, August–November 1987.

	Ship		
	Jordan	*MacArthur*	Total
Ommastrephidae	14,445	495	14,950
Argonauta sp.	16	36	52
unid. squid	9	3	12
Liocranchia sp.	1	9	10
Abraliopsis sp.	9	0	9
Onykia? sp.	4	2	6
Chiroteuthis sp.	3	0	3
Pterygioteuthis sp.	2	0	2
Chtenopteryx sp.	1	1	2
Enoploteuthis? sp.	1	1	2
Abralia? sp.	1	0	1
Thysanoteuthis rhombus	1	0	1
Cranchia scabra	1	0	1
Leachia sp.	1	0	1
Octopodidae	0	1	1
Total	14,495	548	15,043

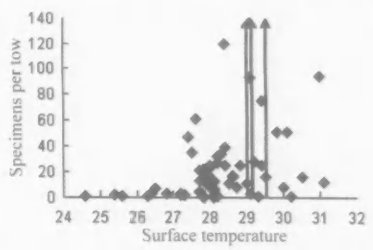

Figure 2

Rhynchoteuthion squid paralarval abundance plotted against surface temperature for NOAA Ship *D.S. Jordan* cruise 8710. Vertical arrows represent samples with maximum numbers of paralarvae.

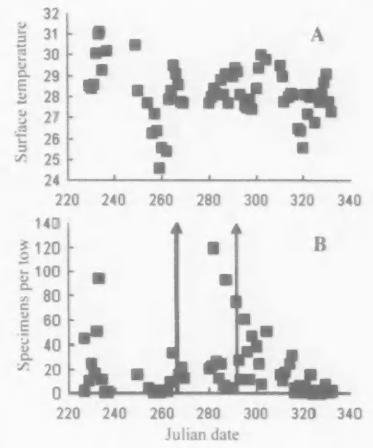

Figure 3

Relationships among water temperature, squid abundance, and date for NOAA Ship *D.S. Jordan* cruise 8710: (**A**) surface temperature plotted against Julian date; (**B**) rhynchoteuthion squid paralarval abundance plotted against Julian date. Vertical arrows represent samples with maximum numbers of paralarvae.

set) and night tows to determine the contribution of diel variability, from either visual avoidance of the net or vertical migration by larger animals, to the size distribution. The overall size distribution was skewed toward the size of newly hatched animals, with the model length 1.0–1.5 mm DML. The size range in dusk samples was 0.5–3.5 mm DML (Fig. 4A). A small second group of larger squid 3.5–8.5 mm DML (modal length ca. 6.0–6.5 mm DML) not present in dusk tows was collected at night in addition to the smaller paralarvae (Fig. 4B). Some stations, such as *Jordan* station IV-05 (Fig. 4D), included only very small squid 1–2 mm DML, as might be expected from a hatching event. The greatest abundance, however, at station III-62, was characterized by a broader range of lengths (Fig. 4C) with a larger modal size of 2.0–2.5 mm DML. On the basis of analysis of growth rings in statoliths from Hawaiian *S. oualaniensis*, a 2.5-mm-ML paralarva is ca. 20 days old (Bigelow, 1991). I therefore conclude that this very high abundance did not result from the net happening upon an egg mass, either just before or just after hatching, but instead an aggregating mechanism must be responsible for this patch.

I examined the second alternative by calculating the variability in flow meter revolutions among tows. The mean and standard deviation for this estimate of sampling efficiency were 2771 and 645, respectively. None of the three outliers from this distribution (one high and two very low) collected >20 rhynchoteuthions. All of the samples with abundances >40 rhynchoteuthions came from tows with 2612–2947 revolutions. Although this parameter can be used to estimate the volume of water filtered by the sample, I did not do this because assumptions about the orientation of the net mouth with respect to the sea surface are required for surface samples and this orientation can change greatly with sea

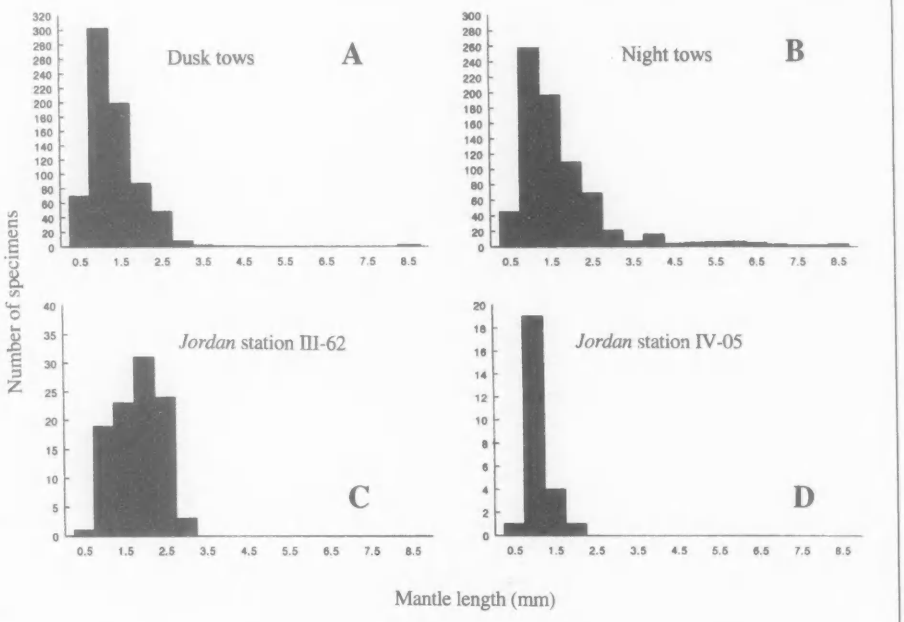

Figure 4

Size-frequency distributions for ommastrephid paralarvae. All specimens were measured from samples that collected <100 rhynchoteuthions. A subsample of 100 specimens was measured from samples containing >100: (**A**) pooled distribution for all dusk tows (samples collected <1 h after local sunset); (**B**) pooled distribution for all night tows (samples collected >1 h after local sunset); (**C**) lengths of 100 specimens from the station that collected maximum abundance; (**D**) example of size-frequency distribution expected from a station that sampled a recent hatching event.

state. The low variability of flow meter counts indicates that observed abundances did not result from sampling artifacts.

Discussion

Aside from the band of high rhynchoteuthion abundance parallel to the coast and coincident with the 29°C isotherm, these collections are not unusual for surface samples of cephalopod paralarvae. The abundance of other cephalopods with paralarvae typically found at the surface, such as *Argonauta*, was not exceptional. Unusually high abundances in these samples were found only in the paralarvae of ommastrephid squids.

The Humboldt squid, *Doscidicus gigas*, is an ommastrephid sufficiently abundant in this area to support commercial fisheries, but descriptions of the paralarvae of this species are not adequate to identify them with confidence. However, the general morphology, morphometrics, and chromatophore patterns of the paralarvae reported here are consistent with those of another widely distributed and abundant ommastrephid, *Sthenoteuthis oualaniensis*, whose paralarvae have been described from off Hawaii (Harman and Young, 1985). It is not possible at this time to be certain which of these species composed the high abundances reported here. Although natural spawning has not been observed directly for either of these species, ommastrephids are known to spawn large egg masses that are gelatinous and pelagic and are very difficult to collect with nets. Spawning aggregations of *S. oualaniensis* and other ommastrephids have been located in other areas. It seems reasonable to assume that either species may aggregate in the study area to produce egg masses.

No information is available on the abundance of these squid paralarvae in subsurface waters of this region. The highest abundance of *S. oualaniensis* in Hawaiian waters is found in the mixed layer from the surface to 20 m depth (Young and Hirota, 1998). Surface abundance therefore appears to be a reasonable indication of overall paralarval distribution of this species. Furthermore, the depth of maximum zooplankton abundance in the eastern tropical

Pacific is generally limited by an oxygen minimum layer beneath the thermocline (Saltzman and Wishner, 1997). Thus, the distribution of these shallow-living paralarvae may have been compressed toward the surface by the oxygen-minimum layer.

Expendable bathythermograph measurements by the *Jordan* during this period showed the mixed-layer depth to be 20–40 m, except where the thermocline was depressed within an anticyclonic eddy located very close to the stations with maximum squid abundance (Hansen and Maul, 1991). Convergence of surface currents associated with the downwelling that depresses the thermocline could aggregate surface plankton such as these paralarvae (Bakun and Csirke, 1998). Although the area of maximum abundance was near the Costa Rica Dome, an upwelling feature where the thermocline typically shoals from 60 m to 30 m depth (Balance et al., 1997), thermal topography in this area was anomalously flat during El Niño of 1987 (Fiedler et al, 1992).

A few other records of cephalopod distribution and abundance are known from this region. In an extensive multicruise survey of the eastern tropical Pacific in 1967–68 (Okutani, 1974), few *S. oualaniensis* or other ommastrephids were collected. Similarly, in a cruise in this region from October 1969 through February 1970, during which surface zooplankton were sampled, no large numbers of paralarvae were encountered, although the most abundant cephalopod family sampled was the Ommastrephidae (Ueynagi and Nonaka, 1993).

Typical numbers of cephalopod paralarvae taken in zooplankton samples worldwide number 0 to perhaps 20 squids per sample, usually about 1–5 squids (Vecchione, 1987). The highest abundance previously reported anywhere of which I am aware was almost 1000 loliginid paralarvae in a 15-min surface plankton tow in the western North Atlantic (Vecchione et al., 1986). The maximum abundance found in the present study was over an order of magnitude greater than that.

The samples reported in this study were collected during the peak of a moderate El Niño event (McPhaden and Hayes, 1990). Surface temperatures in the area averaged 3.5°C warmer than during the same period of the following year (Fiedler et al., 1992). The temperature distribution of these samples indicates that high abundances of rhynchoteuthions would not be expected at temperatures <27.5°C. Therefore, warm El Niño waters probably were the primary reason for the high abundance of squid paralarvae found here. These abundant surface-dwelling paralarvae may have been concentrated to extraordinary densities by convergent surface currents in the vicinity of an anticyclonic eddy. Seasonal occurrence is likely important, because surface temperatures remained high until the end of these cruises, whereas squid abundance decreased dramatically during the final 30 days. The sampling fortunately was conducted during the season when these squid were hatching.

Acknowledgments

These samples and data were collected by biologists from the Marine Mammal Program of the National Marine Fisheries Service Southwest Fisheries Science Center (SWFSC), primarily by R. Pitman and J. Carretta. The samples were sorted in R. Charter's laboratory at SWFSC, and he and G. Moser, also of SWFSC, sent the cephalopods to me. I was assisted in cephalopod sorting and measuring by K. Jackson. The following people provided helpful comments on a draft of this paper: R. Young, G. Moser, B. Collette, and C. Roper. In addition, R. Young graciously provided unpublished data on vertical distribution of Hawaiian paralarvae for an early draft of this paper.

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Early life history stages of the whitetip flyingfish, *Cheilopogon xenopterus* (Gilbert, 1890) (Pisces: Exocoetidae)

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Abstract.–The whitetip flyingfish, *Cheilopogon xenopterus*, is an epipelagic resident of tropical and subtropical eastern Pacific waters. Its eggs are spherical, average 1.8 mm in diameter, and have an homogeneous yolk and no oil globule. About 53 filaments averaging 1 mm in length are evenly distributed on the chorion. The notochord flexes, fin-ray formation is nearly complete, and the characteristic larval pigmentation pattern is established prior to hatching at a larval length of about 2.8–3.3 mm. Larvae hatch with pigmented eyes, functional mouth, and little remaining yolk. Pectoral- and pelvic-fin rays initially are short but elongate rapidly to ca. 25–50% and 20–40% of body length, respectively. A pair of mandibular barbels form at about 4 mm and fuse mesially at about 8 mm. Scales begin to form along the lateral line at about 13–14 mm and cover the body by 26 mm.

The characteristic pigment pattern, visible through the early juvenile stage, consists of the following: melanophores scattered over the mid- and hindbrain, continuing posteriorly as two rows (increasing to four or more rows) along the dorsal margin; a row of melanophores on the horizontal septum of the tail (after hatching); a patch on each side over the hypural area; and two rows along the anal-fin base. Internal pigment is present on the mid- and hindbrain, over the gut, and over the notochord. The pectoral and pelvic fins are sparsely pigmented at hatching and become increasingly pigmented with growth. A barred pigment pattern begins to develop on the body at about 8 mm and by the juvenile stage about six bars are present.

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Flyingfishes, surface-oriented residents of all warm oceans, are well known for their ability to leap from the water and glide over long distances. Flyingfishes can be abundant locally, many are attracted to light, and the gustatory quality of their flesh is generally good (Heemstra and Parin, 1986; Gillett and Ianelli, 1991; Parin, 1995). Directed fisheries for flyingfish currently exist, primarily in parts of the Indo-West Pacific and Caribbean; few such fisheries exist elsewhere (Gillett and Ianelli, 1991; Oxenford et al., 1995; Parin, 1995).

The family contains eight or nine genera and about 50–60 species (Nelson, 1994; Dasilao et al., 1996); nearly half the species are in the genus *Cheilopogon* (Heemstra and Parin, 1986). Eggs have been described for nine *Cheilopogon* species (Barnhart, 1932; Hubbs and Kampa, 1946; Miller, 1952; Imai, 1959; Gorbunova and Parin, 1963; Parin and Gorbunova, 1964; Kovalevskaya, 1965; Gibbs and Staiger, 1970; Vijayaraghavan, 1975; Shigonova and Kovalevskaya, 1991; Watson, 1996), and at least some larval stages are known for 16 species (Hildebrand and Cable, 1930; Barnhart, 1932; Breder, 1938; Hubbs and Kampa, 1946; Imai, 1959, 1960; Gorbunova and Parin, 1963; Kovalevskaya, 1965, 1975, 1977, 1982; Vijayarhagavan, 1975; Chen, 1987, 1988; Shigonova and Kovalevskaya, 1991; Belyanina, 1993; Parin and Belyanina, 1996; Watson, 1996). The purposes of this paper are to provide a description of the egg, larval, and early juvenile stages of the endemic eastern Pacific species *Cheilopogon xenopterus* (Gilbert, 1890) and to compare these briefly with the early stages described for other *Cheilopogon* species in the eastern Pacific.

Materials and methods

Descriptions are based on 20 eggs and a size series of 45 larvae (2.8–22.8 mm) and 8 juveniles (25.9–44.8 mm). Neustonic eggs and larvae and three of the juveniles were collected with Manta nets (Brown and Cheng, 1981) during Marine Mammals Division (Southwest Fisheries Science Center) dolphin surveys in the eastern tropical Pacific (Thayer et al., 1988a, 1988b; Lierheimer et al., 1989, 1990; Philbrick et al., 1991, 1993). The Manta samples were taken nightly from late July through early November or December, 1987–90, and 1992, between about 2–16°N and east of about 115°W. A few juvenile and adult specimens of *C. atrisignis*, *C. dorsomaculata*, *C. furcatus*, *C. papilio*, *C. spilonotopterus*, and *C. xenopterus*, radiographed to make fin-ray and vertebral counts for comparison with counts from series specimens, were obtained from the Scripps Institution of Oceanography Marine Vertebrates Collection (SIO).

Eggs, larvae, and juveniles (except those used exclusively for radiography) were measured to the nearest 0.04 mm by using a Wild M-5 binocular microscope equipped with an ocular micrometer. Dimensions measured for eggs included chorion diameter, maximum yolk diameter, and lengths of the shortest and longest intact chorionic filaments, and for larvae and juveniles, body length (BL), preanal length (PAL), head length (HL), snout length (SnL), barbel length (BbL), eye diameter (ED), head width (HW), body depth (BD), and lengths of the pectoral (P_1L) and pelvic (P_2L) fins. All these dimensions, except chorionic filament length (measured along the axis of the filament from its point of attachment on the chorion to its free tip), are defined by Moser (1996). Larval lengths refer to formalin-preserved body length. All descriptions of pigmentation refer solely to melanistic pigment.

One late embryo (3.3 mm) dissected from the egg and eight larvae (2.9–16.8 mm) were cleared and stained with alcian blue and alizarin red S according to the method of Taylor and VanDyke (1985) to elucidate the development of the axial skeleton and fins and to aid in making counts. Illustrations were made with a Wild M-5 microscope equipped with a camera lucida.

Identification

Specimens were identified by the series method. A size series of larvae and juveniles, linked by shared morphological, meristic, and pigmentation characters, was traced down to recently hatched larvae from juveniles that could be identified by using known juvenile and adult characters. The smallest larvae shared a pigmentation pattern with late-stage embryos that allowed identification of the eggs.

Of the eight flyingfish genera in the eastern tropical Pacific (Parin, 1995; Dasilao et al., 1996), only *Cheilopogon* has paired mandibular barbels during at least part of the larval and juvenile stages (Parin, 1961a, 1961b; Collette et al., 1984). (*Parexocoetus brachypterus* develops a pair of mandibular barbels, and a small beak as well, during the juvenile stage: Collette et al., 1984.) Of the nine *Cheilopogon* species in and near the area (Table 1; Parin, 1995), larvae are known for five: (*C. atrisignis*: Chen, 1987, 1988; *C. furcatus*: Hildebrand and Cable, 1930; *C. heterurus hubbsi*: Barnhart, 1932; Watson, 1996; *C. pinnatibarbatus californicus*: Hubbs and Kampa, 1946; Watson, 1996; and *C. spilonotopterus*: Kovalevskaya, 1977; Chen, 1987, 1988). All five differ from the series treated here. *Cheilopogon rapanouiensis* was eliminated from consideration by its higher vertebral, pectoral-fin ray, and predorsal scale counts (45–46 vs. 43, 16–17 vs. 13–15, and 31–33 vs. 27–28, respectively). *Cheilopogon papilio* was eliminated because of its lower dorsal-fin ray count (9–10 vs. 12–13), usually lower pectoral-fin ray count (12–13 vs. 13–15), because of separate rather than fused barbels and much heavier pectoral- and pelvic-fin pigmentation in the juvenile stage, and because of restricted distribution in coastal waters and the lower Gulf of California (Parin, 1995). The remaining two species, *C. dorsomaculata* and *C. xenopterus*, are widely distributed in the eastern tropical Pacific (Parin, 1995), are quite similar in appearance as small (<ca. 40 mm) juveniles, and both were considered as possible identifications for the present series. Predorsal scale counts from the largest series juveniles (27–28 scales) are consistent with *C. xenopterus* and slightly high for *C. dorsomaculata* (Table 1). Pectoral-fin ray counts for series specimens having full complements of rays (>9 mm; 13–15 rays) match the range for *C. xenopterus* and fall below to within the lower half of the range for *C. dorsomaculata* (Table 1). Juvenile *C. dorsomaculata* typically have less pelvic-fin pigment than *C. xenopterus*, and in this character the larger series specimens are consistent with *C. xenopterus*. Thus, I concluded that the series is *C. xenopterus*.

Specimens examined

Listings are given as cruise and station number or SIO catalogue number, and in parentheses number of specimens and size range. Specimens listed with cruise numbers are housed at the National Marine Fisheries Service Southwest Fisheries Science Center; specimens with SIO numbers are housed at the Scripps Institution of Oceanography Marine Vertebrates Collection.

Cheilopogon xenopterus (Gilbert, 1890).

Eggs: 8910JD: 3-100 (3: 1.8–1.9 mm), 3-102 (7: 1.8–1.9 mm), 4-107 (1: 1.7 mm); 9210JD: 1-001 (4: 1.8–1.9 mm), 1-008 (4: 1.8–1.9 mm), 3-047 (1: 1.8 mm).

Larvae: 8710JD: 1-009 (1: 15.2 mm), 2-016A (1: 2.8 mm), 3-046 (6: 3.4–4.8 mm), 3-054 (1: 2.9 mm), 3-056 (1: 4.9 mm), 3-075 (1: 2.9 mm), 3-078 (2: 5.3, 14.3 mm); 8710M4: 1-003 (1: 4.1 mm); 8810JD: 2-049 (1: 8.0 mm), 3-086 (1: 7.5 mm), 3-118 (5: 8.7-13.6 mm), 4-153 (1: 8.3 mm); 8910JD: 1-015 (1: 2.9 mm), 1-019 (1: 6.4 mm), 1-021 (1: 13.7 mm), 2-056 (1: 6.8 mm), 3-104 (1: 4.8 mm); 8910M4: 1-010 (1: 12.5 mm), 1-012 (1: 3.4 mm), 4-143 (2: 9.8, 13.9 mm); 9010JD: Manta 54 (1: 13.4 mm), Manta 65 (1: 6.4 mm), Manta 74 (1: 22.8 mm); 9210JD: Manta 2 (1: 8.1 mm), Manta 9

Table 1

Selected meristic characters for the *Cheilopogon* species that occur in and near the eastern tropical Pacific Ocean. The pectoral-fin ray count includes the small, spine-like first pectoral-fin ray. Data are from Parin (1960, 1961a), Watson (1996), and counts made during this study. D = dorsal; A = anal; P_1 = pectoral; Proc.C = procurrent caudal-fin rays.

Species	Vertebrae			Fin rays				Predorsal scales
	Abdominal	Caudal	Total	D	A	P_1	Proc. C	
atrisignis	28–30	15–16	43–45	13–15	9–10	13–15	6+8	31–40
dorsomaculata	28–29	14–15	42–44	11–14	9–10	14–17	5–6+6–7	23–25
furcatus	29–31	14–15	43–46	12–14	9–11	14–18	7+6–8	27–35
heterurus hubbsi	31–33	15–17	47–49	12–14	8–11	14–16	6–7+7	28–36
papilio	28–29	14–15	42–44	9–10	9–10	12–13	4–5+6	29–33
pinnatibarbatus californicus	31–35	16–17	48–51	9–13	9–12	14–15	5–6+6–8	40–43
rapanouiensis	30–31	15–16	45–46	11–12	10–11	16–17		31–33
spilonotopterus	29	14	43	13–14	10–11	13–15	6+7	29–34
xenopterus	27–30	13–15	42–44	10–13	9–10	13–15	5–6+6–8	27–30

(1: 6.3 mm), Manta 11 (2: 4.7, 5.3 mm), Manta 19(?) (1: 8.1 mm), Manta 34 (2: 5.3, 5.6 mm), Manta 37 (1: 16.5 mm), Manta 47 (1: 6.5 mm), Manta 51 (1: 6.8 mm); SIO 63-54 (1: 18 mm).

Juveniles: 8710JD: 1-006 (1: 25.9 mm); 8810JD: 3-108 (1: 44.8 mm); 8910JD: 1-039 (1: 36.4 mm); SIO 63-31 (1: 116 mm); SIO 63-96 (1: 38.5 mm); SIO 63-105 (7: 34.5–57.0 mm); SIO 63-608 (3: 64–92 mm); SIO 64-539 (1: 62 mm); SIO 72-121 (2: 42, 45 mm); SIO 73-400 (3: 63–76 mm).

Cheilopogon atrisignis (Jenkins, 1903). SIO 79-29 (1: 52 mm).

Cheilopogon dorsomaculata (Fowler, 1944). SIO 52-399 (1: 46 mm); SIO 52-416 (6: 147–214 mm); SIO 58-318 (1: 179 mm); SIO 78-214 (1: 36.5 mm).

Cheilopogon furcatus (Mitchill, 1815). SIO 76-246 (1: 52 mm); SIO 93-89 (1: 183.5 mm FL).

Cheilopogon papilio (Clarke, 1936). SIO 58-395 (2: 65–75 mm); SIO 69-387 (2: 20, 21 mm); SIO 93-95 (2: 109, 115.5 mm).

Cheilopogon spilonotopterus (Bleeker, 1866). SIO 60-265 (1: 103 mm); SIO 69-405 (1: 39 mm).

Description of eggs

Morphology

Eggs spherical, average 1.8 mm in diameter (range 1.7–1.9 mm), have narrow perivitelline space (mean yolk diameter 1.7 mm, range 1.5–1.8 mm), homogeneous yolk, and lack oil globules (Fig. 1). Between about 42 and 64 slender filaments (mean 53) evenly distributed over smooth, transparent chorion; each attached to chorion at one end and all of similar length (mean 1.2 mm, range 0.7–1.4 mm).

Pigmentation

Chorion unpigmented, yolk colorless to pale yellow. Embryonic pigmentation first appears about midway through development (stage VIII; embryonic tail length increases from 50% to 100% HL during this stage; e.g. Moser and Ahlstrom, 1985) as one to few small melanophores dorsolaterally on midbrain area and small cluster just anterior to each pectoral-fin bud (Fig. 1B). Pigmentation increases dorsolaterally on head, forms around margins of eyes and ventrally on head in stage IX (tail > HL but < 50% yolksac length). During this stage melanophores spread posteriorly and dorsally from prepectoral clusters, forming two rows on dorsum to midway along embryonic axis, and melanophores form dorsally on developing gut, beginning posteriorly early in stage. By stage X (tail extends 50–75% of yolksac length) characteristic larval pigment pattern clearly visible, with dorsal rows extending to near end of tail, a few melanophores around margin of caudal peduncle, and two rows along base of anal fin (Fig. 1C). Near end of embryonic development (stage XI: tail extends >75% of yolksac length) melanophores fill in over central axis of head, form near distal margins of pectoral fins and proximally on caudal fin, may form near distal margins of pelvic fins (present in one of three stage-XI specimens examined), form in internal series over notochord and posteriorly under notochord, and become increasingly dense on dorsal and ventral margins near midtail. Eyes become fully pigmented during stage XI.

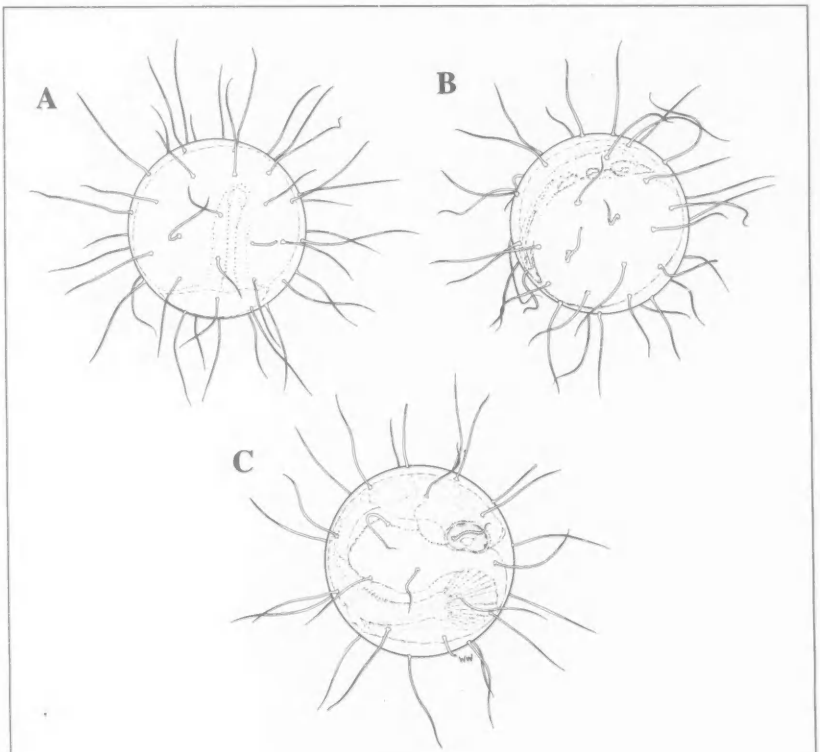

Figure 1

Eggs of *Cheilopogon xenopterus*. (**A**) stage VI, 1.8 mm (8910JD, station 3-102); (**B**) stage VIII, 1.8 mm (9210JD, station 1-008); (**C**) stage X, 1.9 mm (8910JD, station 3-100).

Description of larvae

Morphology

Larvae hatch at about 2.9–3.3 mm length and have little remaining yolk, functional mouth, fully flexed notochord, and rays forming in all fins (Fig. 2). Larvae moderately elongate, with preanal length near 80% BL at hatching, become increasingly elongate with preanal length decreasing to near 70% BL by ca. 8 mm (Table 2). Eyes initially oval (vertical axis about 70% horizontal axis), gradually becoming nearly round. Pectoral- and pelvic-fin rays initially short (near 10% BL), rapidly elongate to ca. 25–50% and 20–40% BL, respectively. Height of dorsal fin increases from about 15% BL in large larvae (15–18 mm) to about 28% BL in small juveniles (by ca. 36 mm). A pair of mandibular barbels forms at about 4 mm. Barbels originate as low, anteroventral thickening that elongates into a slender, flattened flap on each side of lower jaw. Barbels broaden, develop frilled margins, and fuse mesially at their bases by about 8.3 mm (Figs. 2–4). Scales form along lateral line beginning at about 13–14 mm and cover body by 26 mm. There are 27–30 predorsal scales and seven scale rows between dorsal-fin origin and lateral line.

Vertebral column and fin development

Notochord flexion begins during embryonic stage VIII (dorsal, anal, caudal finfolds first visible in this stage) and is completed early in stage IX. Vertebral column ossification begins soon after hatching. Neural and haemal arches and spines apparently form first, before corresponding vertebral centra. Ossification of arches apparently anterior to posterior: in 3.8-mm specimen all arches ossifying except last three neural arches, last haemal arch, and last three or four neural and haemal spines (all present as cartilage). Direction of ossification of individual arches apparently distad from base: in 3.8-mm specimen haemal arches 11–13 appear to be ossifying from near base

Table 2

Summary of measurements of *Cheilopogon xenopterus*, expressed as percentage of body length (BL) or head length (HL). For each measurement the mean is given above and the range is given below. For eye diameter (ED), eye length is given first and eye height second; *n* = number of specimens. Specimens 24.1 mm and larger were considered juveniles. PAL= preanal length; P_1L = pectoral-fin length; P_2L = pelvic-fin length HW = head width; SnL = snout length; BbL = barbel length.

BL (mm)	*n*	PAL/BL	BD/BL	HL/BL	P_1L/BL	P_2L/BL	HW/HL	SnL/HL	ED/HL	BbL/HL
2.8–4.0	9	76	24	33	28 (*n*=6)	28 (*n*=5)	69	14	42,31	0.3
		71–88	22–28	30–39	12–35	18–32	67–74	12–17	39–47, 28–34	0–3
4.1–6.0	10	72	21	30	38 (*n*=8)	38 (*n*=9)	69	17	41,33	4 (*n*=9)
		68–75	19–24	29–33	27–50	34–44	66–75	13–23	38–45, 29–35	2–10
6.1–8.0	8	70	18	26	37 (*n*=5)	30	67	17	41,34	17 (*n*=7)
		68–73	17–20	24–28	35–40	28–33	63–73	14–20	38–42, 31–37	10–24
8.1–10.0	6	69	17	24	39 (*n*=5)	35 (*n*=5)	66	17	43,36	36
		66–71	16–18	23–25	35–43	30–39	61–72	16–19	40–46, 33–42	24–48
10.1–12.0	2	68	17	22	40(*n*=1)	31	67	16	44,37	46
		68–68	16–17	22–22		30–32	67–67	16–17	43–44	39–53
12.1–14.0	5	68	15	20	42	35	71	18	46,42	49
		66–68	14–16	19–20	39–46	34–37	68–73	16–19	43–48, 39–45	39–57
14.1–16.0	2	73	16	21	48	39	73	15	47,43	65
		72–75	16–17	20–21	46–49	37–41	70–76	13–17	44–50, 42–43	59–72
16.1–18.0	2	68	16	20	50	41	74	20	45,43	71
		68–68	15–18	19–20	49–52	41–41	73–75	17–22	44–47, 41–45	59–83
22.1–24.0	1	68	15	20	58	39	71	20	46,45	61
24.1–26.0	1	69	15	19	56	39	76	18	48,47	55
34.1–36.0	1	71	16	21	65	43	70	24	38,37	43
36.1–38.0	1	72	16	20	68	44	73	17	42,44	44
38.1–40.0	1	74	15	22	72	43	67	18	36,36	43
40.1–42.0	2	72	16	22	67	42	67	21	39,40	46
		71–73	15–16	22–22	67–68	41–42	66–68	20–23	36–41, 38–42	39–53
42.1–44.0	1	71	16	22	69	43	66	20	38,37	39
44.1–46.0	1	77	19	21	72	42	79	19	43,44	53

of each haemapophysis. In 6.3-mm specimen last four neural arches and spines broadening and by 8.2 mm last six much broader than more anterior neural arches and spines. These broad posterior neural arches and spines provide the necessary attachment surfaces for the large supracarinalis posterior, flexor dorsalis, and flexor ventralis muscles (Winterbottom, 1974; Dasilao et al., 1996) which are involved in generating the strong caudal thrust required for gliding.

Ossification of each vertebra begins ventrally. As bone spreads dorsad from ventrum, ossifications also form at bases of the two neurapophyses and spread mesially and ventrad to complete centrum. Centra apparently added from anterior to posterior, but urostyle and penultimate centrum ossify before other caudal vertebrae. All vertebrae ossified by 5.2 mm (Table 3). There are 42–44 vertebrae: 27–30 abdominal and 13–15 caudal (modally 29 + 14 = 43).

Pleural ribs first visible in 6.3-mm specimen (Table 3). These ossify adjacent to parapophyses beginning at third vertebra (at second vertebra on one side in one specimen) and are added posteriorly. Epineural intermuscular bones begin ossifying in myosepta anteriorly, initially remote from vertebrae, by 8.2 mm (Table 3), and pairs added posteriorly. Ossification of each rib and epineural intermuscular bone is both mesial toward adjacent parapophysis, and distal. Full complements of both series not yet formed in largest cleared and stained specimen.

Caudal and pectoral are first fins to begin forming. Hypural elements first visible in late stage-VIII embryos, begin ossifying soon after hatching (by 2.9 mm). Retrorse basal spur forms on hypural 1 by 6.3 mm. Uroneural ossifying by 5.2 mm and epurals 1 and 2 by 6.3 mm. Epural 3 not clearly ossifying until 8.2 mm. Principal caudal-fin rays begin to form

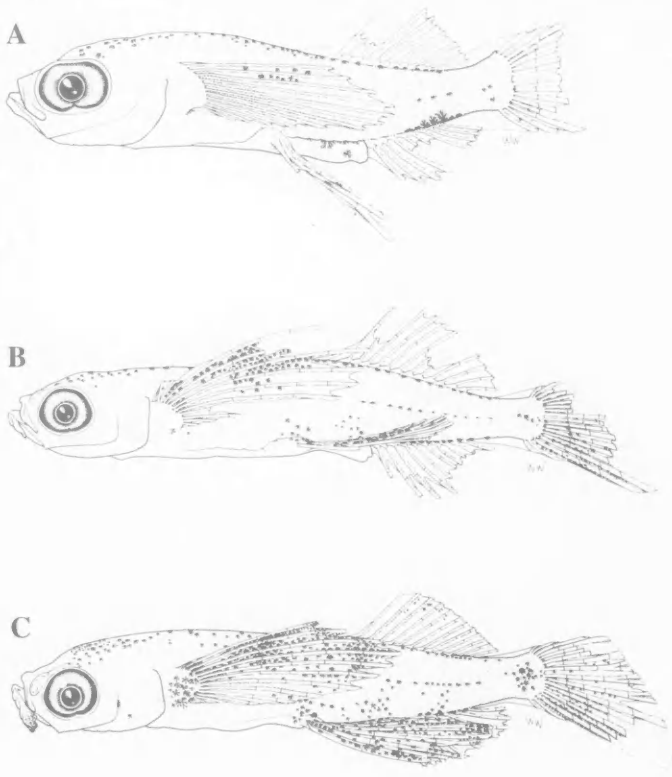

Figure 2

Larval *Cheilopogon xenopterus*, lateral view. (**A**) 3.5 mm (8710JD, station 3-046); (**B**) 8.0 mm (8810JD, station 2-049); (**C**) 8.1 mm (9210JD, station Manta 2). Fin rays shown in dotted lines are based on fins of other specimens of similar size.

during embryonic stage X (Table 3) and all 7+8 rays present at hatching. All principal rays supported by hypurals through at least 8.2 mm but by 10.5 mm lowermost principal ray partially supported by haemal spine associated with preural centrum 1. By 13.4 mm lowermost principal ray fully supported and adjacent principal ray partially supported by haemal spine, and by 16.8 mm both rays fully supported by haemal spine. Procurrent caudal-fin rays begin to form shortly after hatching (by 3.8 mm) but full complement of 5–6 dorsal and 6–8 ventral rays not attained until near end of larval development (by 16.8 mm). Caudal fin initially rounded, becomes assymetrical as lower principal rays elongate, beginning at about 5 mm.

Pectoral-fin buds form in stage-VIII embryos, almost simultaneously with beginning of notochord flexion, and upper rays form during embryonic stage X. Addition of rays is ventrad, with full complement of 13–15 rays (including uppermost small, spine-like ray) attained by 9.3 mm (Table 3). Lowermost ray quite small and nearly completely covered by scales in juveniles larger than

Table 3

Counts for cleared and stained *Cheilopogon xenopterus*. In cases where two counts are given for one category, the first value is the count from the left side, the second is from the right side. Pectoral fin-ray counts include the first small, spine-like ray. D = dorsal; A = anal; P_1 = pectoral; P_2 = pelvic; C = caudal.

	Vertebrae					Fin rays				
BL (mm)	Abdominal	Caudal	Pleural ribs	Epineural inter-muscular	Branchiostegal rays	D	A	P_1	P_2	C
3.3 (embryo)	0	0	0	0	2	0	0	3	5	0+5+5+0
2.9	0	0	0	0	2	11	10	6	6	0+7+8+0
3.8	23	2	0	0	6	12	10	13	6	1+7+8+1
5.2	28	15	0	0	7	12	10	11	6	2+7+8+2
6.3	29	14	12	0	7,8	13	10	12	6	2+7+8+2
8.2	29	14	15	8	9	12	9	12	6	3+7+8+3
10.5	29	14	17	14	9	12	11	13	6	3+7+8+4
13.4	28	15	20,21	26	9	12	9	15,14	6	4+7+8+6
16.8	28	15	22	29	11	13	9	15	6	6+7+8+7

about 38 mm. Pelvic-fin buds form during embryonic stage IX, at about completion of notochord flexion. All six pelvic-fin rays apparently present at hatching.

Cartilaginous dorsal- and anal-fin pterygiophores form late during embryonic development: cleared and stained late stage-X embryo had six dorsal, five anal-fin pterygiophores. Addition and ossification of pterygiophores apparently anterior to posterior. Each pterygiophore initially is single cartilage which begins to ossify near middle of lower portion (forming proximal radial). Although pterygiophores did not stain well in smaller larvae, at least first three or four anal-fin pterygiophores beginning to ossify in 3.8-mm specimen and first five or six dorsal- and anal-fin pterygiophores in 5.2-mm specimen. By 6.3 mm all but posterior three or four dorsal proximal radials ossifying, and distal radials appear to be ossifying adjacent to fin-ray bases. About 8.2–13.4 mm separate ossifications, probably representing middle radials, form on cartilage between proximal and distal radials, but by 16.8 mm each proximal + middle radial appears to be a single ossified unit. Dorsal- and anal-fin rays begin to form in stage-XI embryos; all anal- and most dorsal-fin rays present at hatching.

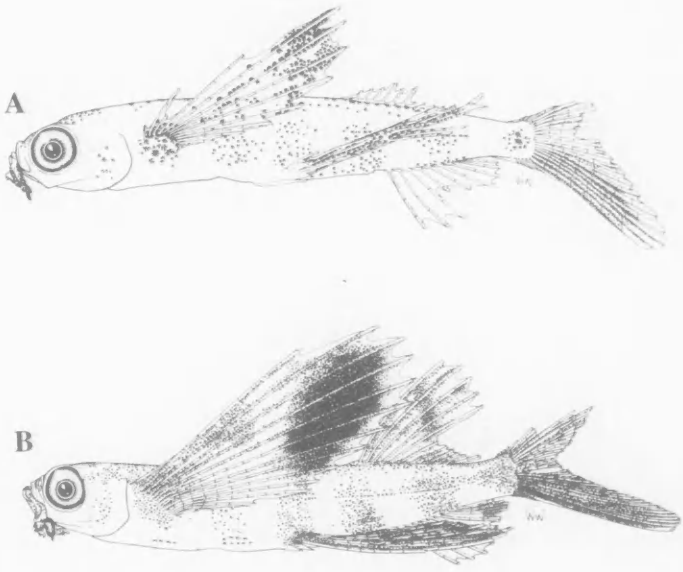

Figure 3

Cheilopogon xenopterus, lateral view. (**A**) larva, 12.5 mm (8910M4, station 1-010); (**B**) juvenile, 36.4 mm (8910JD, station 1-039). Fin rays (and fin pigment in A) shown in dotted lines are based on fins of other specimens of similar size.

Pigmentation

Most elements of basic pattern established during late embryonic development are visible throughout larval period. Principal internal elements of pattern are 1) melanophores under mid- and hindbrain (difficult to see after about 6 mm); 2) row over notochord (difficult to see after about 6 mm); 3) melanophores present around urostyle and proximally on hypurals; 4) melanophores present dorsally, dorsolaterally on gut. Principal external elements are: 1) dorsal melanophores covering mid- and hindbrain areas; 2) two somewhat irregular rows along dorsal margin of trunk and tail (increasing to four rows after about 9 mm), and melanophores in each row usually more closely spaced along posterior half of dorsal-fin base; 3) two rows along anal-fin base, commonly expanded along posterior half of fin base; 4) patch on each side over urostyle and hypural area; 5) scattered melanophores on pectoral, pelvic, and caudal fins.

Subsequent additions to internal pigmentation include melanophores spreading around sides of mid- and hindbrain and increasing in number anteriorly over notochord, forming internally on opercular area beginning at about 6–6.5 mm, and spreading ventrolaterally on gut (primarily anteriorly), surrounding gut at level of pectoral-fin bases between 12 and 18 mm. Pigmentation on urostyle and hypural area usually increases somewhat. External dorsal pigmentation on head slowly increases, spreading forward onto snout after about 13 mm. Melanophores form on upper jaw by about 10 mm. In early juveniles, melanophores over mid- and hindbrain spread ventolaterally, reaching level of pectoral-fin origin by about 36 mm. External melanophores present on central opercular area by about 8 mm (Fig. 2C), form indistinct bar across cheek by about 12–15 mm (Fig. 3A). Barbels initially unpigmented, become densely pigmented distally, usually beginning between 6 and 7 mm. As barbels broaden, melanophores become more concentrated along distal margins and after barbel fusion, connecting membrane becomes intensely pigmented along distal margin (by 12–13 mm:

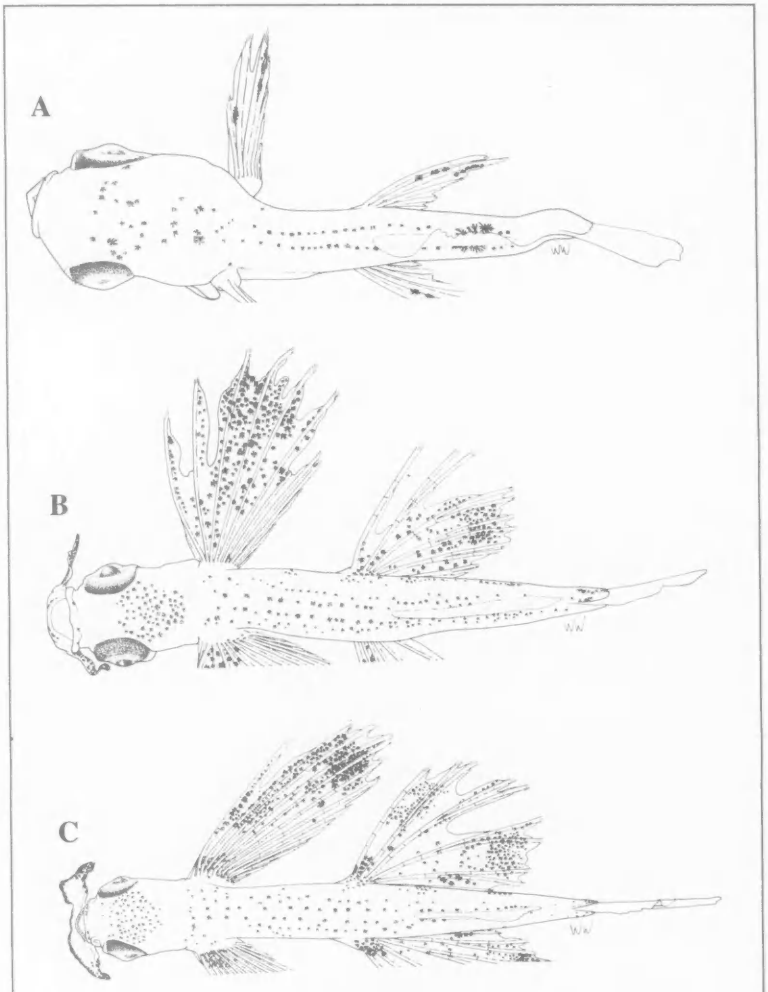

Figure 4

Larval *Cheilopogon xenopterus*, dorsal view. (**A**) 2.9 mm (8910JD, station 1-015); (**B**) 10.5 mm (8810JD, station 3-118); (**C**) 13.4 mm (9010JD, station Manta 54).

Fig. 4C). Few melanophores usually form along lower jaw after about 7 mm.

Soon after hatching, a row of melanophores forms along horizontal septum, originating just behind midtail and spreading cephalad and caudad (primarily cephalad) along tail (Fig. 2, A and B). Barred pattern begins to develop at about 6 mm as melanophores spread upward from pelvic-fin bases and from ventral margins of last three or four preanal myomeres (Fig. 2B). Two more bars begin to spread upward from vicinity of anal-fin rays 5–8 and from midway between pectoral- and pelvic-fin bases (Figs. 2C, 3A) between about 8 and 9 mm. Bars usually do not reach dorsal margin in larvae. Pigmentation on pectoral-fin base sparse until about 8 mm then increases, spreads onto adjacent myomeres, and in juveniles merges with melanophores spreading downward from dorsum to form saddle (Figs. 2C; 3, A and B). Melanophore cluster on hypural area expands to cover almost entire area by about 13 mm. Juveniles thus display six or seven bars (including pectoral saddle); in juveniles >30–40 mm posterior three or four bars most prominent (Fig. 3B).

Pectoral-fin pigmentation initially sparse. After hatching, melanophores gradually spread over membranes between upper 5–6 rays, a few scattered between all but lowermost 3–4 rays, by about 8 mm (Fig. 2, A–C). Pigment patterns variable in larvae

<10–12 mm, except that melanophores tend to be more concentrated near distal margin between upper 5–7 rays and in patch about midway along upper rays. After about 12 mm concentration midway along upper rays commonly persists, but may diminish or disappear, and distal patch expands to form distinct blotch along upper 6–8 rays, bordered by unpigmented (or sparsely pigmented) margin (Fig. 4C). Distal blotch expands into elongate oval band over much of width of pectoral fin in juveniles (Fig. 3B). Upper 4–6 pectoral rays also may remain sparsely to moderately pigmented, especially proximally and in the blotch midway along upper rays, in larger larvae and juveniles. Apart from upper rays and distal blotch or band, remainder of fin has little pigment after ca. 15 mm.

Pelvic-fin pigment may form before hatching; always present after hatching. Sparse initially, commonly sparse to moderate throughout larval development (Fig. 4). Pattern variable: melanophores tend to be more concentrated near distal margin of most or all of fin, in distal patch at innermost ray or between two or three middle rays, or in two distal patches at innermost and outermost rays. Occasionally melanophores more concentrated distally and midway along rays. Distal patch near middle of fin is most common pattern in larger larvae and juveniles.

Caudal-fin pigmentation forms in late embryos, initially proximally, mostly or entirely on lower rays. Pigment increases and spreads to about three-quarters of length of lower principal rays by ca. 8 mm. Melanophores consistently present on upper part of fin by about 8 mm but pigment here is sparse in larvae and sparse to moderate in juveniles.

Diagonal band forms on dorsal fin, originating distally between anterior 2–3 rays just after 8 mm (Fig. 2C) and reaching base of rays 6–7 between 18 and 22 mm. Pigmentation may be sparse in lower (=posterior) part of band and in larger juveniles band appears more like elongate oval patch along first 5–6 rays. Distal blotch forms at last 2–3 rays beginning at about 12–13 mm. Melanophores form on membranes between (primarily adjacent to) first 5–6 rays after 18 mm. Anal fin unpigmented in larvae, but distal blotch forms at last 2–3 rays in juveniles (Fig. 3B).

Comparisons

Eggs

Most exocoetids have spherical eggs that are about 1.5–3 mm in diameter, lack oil globules, and have filaments on the chorion (Collette et al., 1984). *Cheilopogon* eggs are typical exocoetids in these characters. For most of the *Cheilopogon* species the filaments are evenly distributed as in *C. xenopterus*. Only *C. heterurus* and *C. unicolor* have been described as having a different arrangement, with filaments grouped in bipolar clusters (Barnhart, 1932; Miller, 1952; Imai, 1959; Gorbunova and Parin, 1963; Watson, 1996). Among the species with uniform filament distribution, the number of filaments ranges from about 10 to 90; the range in *C. xenopterus* (about 40–60) apparently is typical (e.g. Collette et al., 1984). Filament length in these species ranges from less than 1 mm to just over 10 mm; most commonly the filaments are long, a character shared with *Cypselurus* (e.g. Collette et al., 1984). The short filaments of *Cheilopogon xenopterus* (about 1 mm) are a character shared with *Prognichthys* (Kovalevskaya, 1982) and with at least some of the members of the *C. nigricans* species group (Parin and Belyanina, 1996), which includes *C. dorsomaculata* and *C. xenopterus* in the eastern tropical Pacific. Eggs have not been described for *C. dorsomaculata* or the two *Prognichthys* species in the eastern tropical Pacific (Parin, 1995) and it is unknown how they might be distinguished from the eggs of *C. xenopterus* except that late stage *Prognichthys* embryos should be more densely pigmented. An unidentified type of exocoetid egg (2.2 mm diameter with ca. 150 short filaments) occasionally co-occurs with *C. xenopterus* in plankton samples; it might be one of these species (larval *Prognichthys* are relatively common in the samples).

Collette et al. (1984) noted that some flyingfishes apparently have a preanal finfold during early development and suggested that it is an embryonic feature that is lost soon after hatching. There is no preanal finfold in *C. xenopterus*.

Larvae and juveniles

Larval *Cheilopogon* range between about 4 and 6 mm (e.g. Collette et al., 1984) and are well developed at hatching. *Cheilopogon xenopterus* may be a bit smaller than usual, but otherwise is typical of the genus at hatching. *Cheilopogon* larvae develop a pair of mandibular barbels that persist into the juvenile stage and remain separate or fuse mesially—the membrane joining the barbels either remaining low and simple or becoming broad and fimbriate. Among the *Cheilopogon* species in the eastern Pacific, *C. furcatus*, *C. heterurus hubbsi*, and *C. papilio* retain separate barbels in the juvenile stage. The barbels become fused basally by means of a low, sparsely pigmented or unpigmented membrane in *C. atrisignis* and *C. spilonotopterus*, whereas in *C. dorsomaculata* and *C. xenopterus* the basal membrane is somewhat broader and densely pigmented along its margin.

Only one species, *C. pinnatibarbatus*, is known to have a broad, fimbriate membrane that unites the barbels (Hubbs and Kampa, 1946; Imai, 1959). The barbels become moderately long (Bbl > HL) in *C. atrisignis* and *C. spilonotopterus*, whereas the other species retain relatively short barbels (Bbl < HL). The size and condition of the barbels in *C. rapanouiensis* are unknown, but in the closely related species *C. agoo* they are short (Chen, 1987, 1988).

Larval pigmentation in *Cheilopogon* initially ranges from sparse to dense and typically increases gradually during development. The sparsely pigmented larvae, including *C. xenopterus*, probably *C. atrisignis* and *C. dorsomaculata*, and possibly *C. spilonotopterus* and *C. papilio*, display a pattern primarily of melanophore rows on the dorsum, on the horizontal septum, and on the ventral margin of the tail, and usually bars form in the latter part of the larval stage (Kovalevskaya, 1965, 1977; Chen, 1987, 1988). The more heavily pigmented species, including *C. furcatus*, *C. heterurus hubbsi*, and *C. pinnatibarbatus californicus*, display a pattern similar to that of larval *Cypselurus*, with melanophores more evenly distributed over the trunk and at least anteriorly on the tail (sometimes diminishing to dorsal, midlateral, and ventral rows on the posterior half of the tail) (Hildebrand and Cable, 1930; Hubbs and Kampa, 1946; Watson, 1996). *Cheilopogon rapanouiensis* might belong to this latter group as well, if its larvae resemble the moderately pigmented larvae of *C. agoo* (Chen, 1987, 1988). Juveniles of most species are barred; about six bars (as in *C. xenopterus*) is common.

Larvae and juveniles of *C. xenopterus* usually can be distinguished without great difficulty from the other flyingfish species in the eastern Pacific, except perhaps from *C. dorsomaculata*. The position of the anal-fin origin below dorsal rays 4–7 distinguishes *C. xenopterus* from *Exocoetus*, *Fodiator*, *Hirundichthys*, and *Oxyporhamphus*, in which the anal-fin origin ranges from just ahead of the dorsal-fin origin to under dorsal rays 1–3, depending on species (e.g. Imai, 1954; Kovalevskaya, 1964, 1980; Chen, 1988; Watson, 1996). Larger larvae and juveniles of all four genera are further distinguished from *C. xenopterus* (and all the other *Cheilopogon* species) by their lack of paired mandibular barbels. *Cheilopogon xenopterus* (and all the other flyingfishes) are also distinguished from *Exocoetus* by having much more posteriorly placed pelvic fins. Larval *Fodiator* and *Oxyporhamphus* are unique in developing a beak beginning at about 6 mm and 8 mm, respectively, whereas *Parexocoetus* acquires a much smaller beak in the juvenile stage, by about 18 mm (e.g. Collette et al., 1984; Watson, 1996). *Cheilopogon xenopterus* is rather sparsely pigmented, in contrast to the more general, denser pigmentation of larval *Cypselurus*, *Exocoetus*, *Fodiator*, *Parexocoetus*, *Prognichthys*, and the three or four *Cheilopogon* species noted above (e.g., Hildebrand and Cable, 1930; Imai, 1959, 1960; Kovalevskaya, 1980; Chen, 1988; Watson, 1996). Among the more sparsely pigmented flyingfish larvae, *Hirundichthys* (which may be moderately pigmented initially, but become more sparsely pigmented on at least the prepelvic part of the trunk; e.g. Kovalevskaya, 1980) and *Oxyporhamphus* are easily distinguished from *C. xenopterus* by the characters noted above. In addition, larval *Oxyporhamphus* are more elongate, with much shorter pectoral and pelvic fins, and they lack a row of melanophores along the horizontal septum before about 9 mm (e.g. Khrapkova-Kovalevskaya, 1963; Watson, 1996) in contrast to before 4 mm in *C. xenopterus*. Among the five *Cheilopogon* species in the eastern Pacific with sparsely pigmented (or assumed to be sparsely pigmented) larvae, it usually should be possible to distinguish *C. atrisignis* and *C. papilio* from *C. xenopterus* by a combination of myomere and dorsal, anal, and (in larger larvae) pectoral-fin ray counts (e.g. Table 1). At larger sizes (small larvae have not been described) larval *C. atrisignis* and *C. spilonotopterus* can be distinguished from *C. xenopterus* by barbel structure and pigmentation, and *C. papilio* can be distinguished by barbel structure and fin pigmentation, as noted above. Large larval and juvenile *C. spilonotopterus* are more fully and evenly pigmented on the trunk (by about 14 mm) and lack the barred pattern displayed by larger larval and juvenile *C. xenopterus* (e.g. Kovalevskaya, 1977; Chen, 1987, 1988). *Cheilopogon papilio* likewise become more generally pigmented than *C. xenopterus*, although four or five bars remain visible through at least 21 mm. Juvenile *C. dorsomaculata* smaller than about 40 mm bear a striking resemblance to *C. xenopterus* but can be distinguished by small differences in meristic characters (Table 1) and have more sparsely pigmented (nearly unpigmented) pelvic fins than do *C. xenopterus*. Larvae of *C. dorsomaculata* have not been described, but the similarity of the small juveniles to *C. xenopterus* suggests that it may be difficult to distinguish the larvae of the two species.

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Estimating the harvest of Pacific walrus, *Odobenus rosmarus divergens*, in Alaska

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For thousands of years, walrus hunting has been an important component of the economy and culture of Native communities along the Bering and Chukchi Sea coasts (Ray, 1975). Today, the Pacific walrus (*Odobenus rosmarus divergens*) remains a valuable resource to coastal natives in Alaska (United States) and Chukotka (Russia) as a source of food and raw materials for traditional equipment and handicrafts.

Accurate information regarding the number of animals removed annually from the population is fundamental for the conservation and management of any species. As the agency responsible for managing Pacific walrus in U.S. waters, the U.S. Fish and Wildlife Service (FWS) gathers data on the size and composition of the subsistence walrus harvest in Alaska. The FWS presently administers two separate harvest monitoring programs: the Walrus Harvest Monitoring Project (WHMP) and the Marking Tagging and Reporting Program (MTRP).

The WHMP is an observer program carried out at select walrus hunting villages in Alaska. Each spring, as the pack ice recedes northward, hunters from coastal communities in the Bering Strait region have access to herds of walrus as they migrate to their summer range. Historical harvest information indicates that approximately 80% of the annual reported walrus harvest in Alaska occurs in this region (Fay and Bowlby[1]). WHMP monitors stationed at the primary walrus hunting villages in the Bering Strait region (Gambell, Savoonga, Little Diomede and Wales; Fig. 1) collect information on the size and composition of the walrus harvest. Harvest monitors meet boats as they return from walrus hunting trips in order to collect biological samples and harvest information at the boat landing site (Garlich-Miller[2]). The goal of the WHMP is to identify and record the gender and age class of every walrus retrieved by hunters from these villages during the monitoring period. Although there is no way of evaluating the degree to which this goal is achieved, WHMP monitors meet most of the returning boats, and the number of retrieved animals not recorded during the harvest monitoring period is believed to be small (Dickerson[3]).

The MTRP is a Federally mandated year-round, statewide program (Fig. 1). The marking and tagging rule requires that all hunters certify (tag) walrus ivory (tusks) and report all walruses that are taken. The objectives of the MTRP are to collect harvest information and to certify specified marine mammal parts to help control illegal harvests and trade. Hunters are required to bring walrus tusks to a MTRP tagger within 30 days of the kill. The tagger attaches individually numbered wire tags to the tusks and records the numbers on a tagging certificate. MTRP tags are not attached to calf walruses (or other walruses that may be missing tusks); however, hunters are required to report all animals taken. The age class, gender, kill date, and kill location of each walrus are recorded on the certificate (Stephensen et al.[4]).

These two programs independently provide information on the size and composition of the harvest. Except in the case of the village of Wales, WHMP and MTRP staff are different people. Each of the two monitoring programs has its strengths and weaknesses. The WHMP benefits from the presence of on-site staff to collect accurate biological information from every walrus retrieved in a community during the monitoring period. Unfortunately, the monitoring period is seasonal (restricted to the spring hunt) and operates only in four coastal villages. The MTRP is a statewide, year-round program; however hunter compliance with the MTRP rule is variable and animals lacking tusks (e.g. calves, yearlings, and animals with broken tusks) often go unreported (Burn, 1998).

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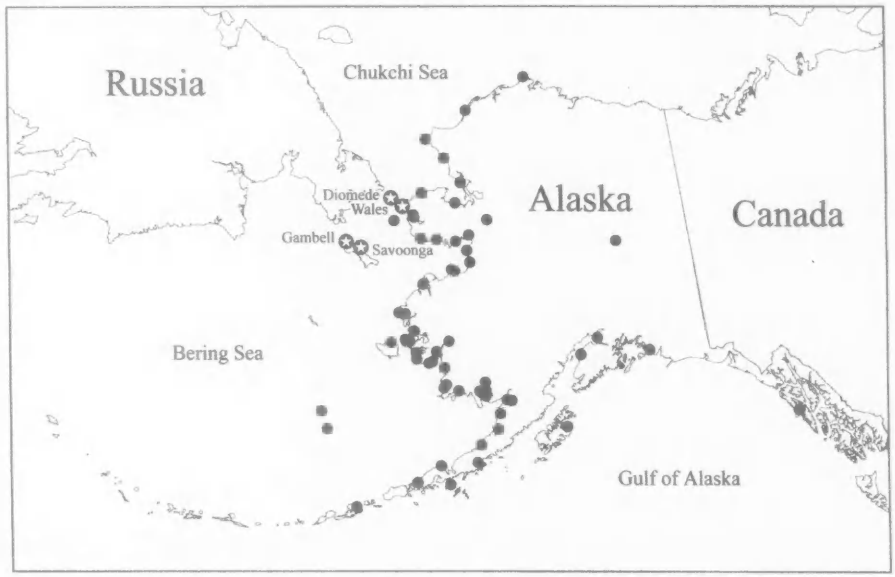

Figure 1

Location of Alaska villages where walrus harvest information is collected through the Walrus Harvest Monitor Project (✪) and the Marking Tagging and Reporting Program (●). Note that tusks may be tagged in selected locations outside the walrus' range.

Owing to funding and logistical constraints that prevent the year-round, statewide implementation of the WHMP and imperfect hunter compliance with the MTRP, not all harvested walruses are recorded. The FWS must therefore rely on analytical methods to estimate the size of the total annual harvest based on the best available information. Here we describe a new method for estimating the size of the annual walrus harvest in Alaska using a correction factor for noncompliance with the MTRP rule.

Materials and methods

Prior to the initiation of the MTRP, the statewide walrus harvest was approximated by using a prediction equation applied to WHMP data. The prediction equation was based upon the historic relationship of the size of the spring harvest at WHMP-monitored villages in relation to the remaining hunting villages in Alaska. This information was obtained from the Alaska Department of Fish and Game, which administered a statewide harvest monitoring program between the years of 1960 and 1978. To estimate the statewide harvest, the FWS used a least-squares regression to describe the relation between the Gambell, Savoonga, and Diomede harvests to the statewide totals. The resulting prediction equation (Equation 1, r^2=0.239) was subsequently used to estimate the total statewide harvest on the basis of data collected annually after 1978 through the WHMP at Gambell, Savoonga, and Diomede.

$$N = 459.7 + 1.26\,(WHMP_{Total}), \qquad (2)$$

where N = total statewide harvest estimate; and
$WHMP_{Total}$ = total number of retrieved walruses recorded during monitored spring hunts at select villages (Diomede, Gambell, and Savoonga) for a given year.

The evolution of the MTRP as a year-round, statewide monitoring program provided the opportunity to improve the reliability of harvest estimates by using current data. Because there is spatial and temporal overlap between the two programs, the WHMP can serve as a baseline for evaluating compliance with the MTRP program. A correction factor for noncompliance can be estimated as a proportion by using the following equation:

$$R = \frac{WHMP_{Total}}{MTRP_{WHMP}}, \qquad (2)$$

Table 1

Walrus harvest data from the Walrus Harvest Monitor Project (WHMP) and Marking, Tagging, and Reporting Program (MTRP), 1992–1997.

Year	$WHMP_{Total}$	$MTRP_{WHMP}$	Correction factor (R)	Standard error SE(R)	$MTRP_{Total}$	Prediction Equation 1	Proportional Equation 3	95% CI of Equation 3
1992	820	976			1700	1491[1]		
1993	710	708	1.003	0.21	1189	1353	1192	703–1682
1994	971	799	1.215	0.17	1328	1681	1614	1171–2056
1995	1204	785	1.534	0.17	1096	1974	1681	1316–2046
1996	1220	773	1.578	0.33	1572	1994	2481	1464–3497
1997	856	574	1.491	0.09	1045	1537	1558	1373–1742

[1] The calculated estimate was less than the value of $MTRP_{Total}$. The $MTRP_{Total}$ was therefore used as a minimum estimate of the statewide walrus harvest.

where R = correction factor for noncompliance; and

$MTRP_{WHMP}$ = a subset of the number of walruses recorded through the MTRP with reported kill dates and locations that coincide with WHMP operations (presumed to have been recorded through both the MTRP and the WHMP).

The standard error of this ratio estimate is calculated according to Snedecor and Cochran (1967, p. 537) by treating each of the three villages as independent estimates of overall compliance. Data from the village of Wales were not used in the analysis because of small harvests and a lack of independence between the WHMP and MTRP programs in that village.

Assuming the estimated compliance with the MTRP is uniform throughout the full range of walrus hunting villages, the total MTRP harvest can be adjusted as follows:

$$N = MTRP_{Total} \times R, \quad (3)$$

where $MTRP_{Total}$ = the total number of walrus recorded through the MTRP.

Results

Data from the MTRP and WHMP are currently available for the years 1992–97 (Table 1). Estimated compliance with the MTRP (the reciprocal of R) ranged from 63% to 99%. Harvest estimates based on the prediction equation and the proportional equation differed depending on the proportion of animals recorded through each of the two monitoring programs. The difference between the two methods was not statistically significant for any year. Comparisons of the 1992 MTRP and WHMP harvest data suggests that the WHMP monitors were unable to account for all the retrieved walruses landed during the monitoring period. In this instance, the $MTRP_{Total}$ was considered the minimum estimate of the statewide harvest.

Discussion

Prior to 1997, the FWS used WHMP data collected annually at Gambell, Savoonga, and Diomede as an index for estimating the total statewide harvest of walrus. One drawback of this method has been that the equation assumes that the relation between the hunting success of WHMP and non-WHMP villages is constant over time (Fay et al., 1997). In fact, recent harvest data have shown that the relative hunting success of each village is highly variable. The annual harvest at each village is subject to large interannual variation, presumably as a result of weather and ice patterns affecting the availability of walruses to hunters at a given geographical location (Garlich-Miller[2]).

One advantage of the proportional equation (Eq. 3) over the prediction equation (Eq. 1) is that it can account for variability in the relative success of hunting villages. For example, on the basis of comparable numbers of walrus recorded through the WHMP in Gambell, Savoonga, and Diomede in 1995 and 1996, the prediction equation produced remarkably similar harvest estimates for the two years (1974 and 1994 walrus, respectively). Although MTRP compliance rates were also comparable for these years, the proportional equation, in which statewide MTRP data were used, produced harvest estimates that were markedly different (1681 and 2481 walrus, respectively). We

believe that this difference, which reflects interannual variability in the hunting success of non-WHMP villages, more accurately reflects statewide harvest levels for these two years. For the reasons stated above, the FWS has adopted the use of the proportional equation to estimate the size of the walrus harvest.

In 1992, the assumption that all retrieved walrus were recorded during WHMP operations was not met. In this instance we considered the uncorrected MTRP data as a minimum harvest estimate for that year. The WHMP was re-initiated in 1992 after a two-year hiatus; the lack of experienced personnel likely contributed to the poor monitoring results that season. Since that time, program managers have attempted to improve the program by hiring experienced monitors and additional village assistants to meet all returning boats and by emphasizing the importance of recording all retrieved animals (Dickerson[3]).

Another assumption of the proportional equation is that compliance in the villages of Gambell, Savoonga, and Diomede is representative of non-WHMP villages. Compliance was variable between villages and years, suggesting that there was little correlation between the two programs. Since conducting analyses of MTRP compliance, information and education efforts in these villages appear to have been effective at increasing compliance. The accuracy of this method could be improved by increasing the number of villages in the WHMP.

In both the prediction and proportional equations, estimates are based on the number of walrus that are retrieved by hunters. Fay et al. (1994) estimated that 42% of walrus struck by hunters are not retrieved and subsequently die at sea. In order to estimate total human-caused removals from the Pacific walrus population, harvest estimates are adjusted to account for animals struck and lost.

Accurate harvest data are vital to the management of the Pacific walrus population. Harvest data are incorporated into stock assessment reports that chart the status and trend of the population. The stock assessment process compares estimates of human-caused mortality with a calculated potential biological removal (PBR) level to determine the status of a stock. One of the reasons a stock may be designated as "strategic" depends upon whether or not its level of human-caused mortality exceeds the calculated PBR level (Wade, 1998). Since 1992, most human caused mortality affecting the Pacific walrus population has been associated with walrus hunting activities in Alaska and Chukotka. Between 1992 and 1996 the combined annual take of walrus in the U.S. and Russia averaged 4869 walrus per year (Gorbics et al.[5]). Russian harvest data are currently unavailable for 1997. Because annual estimates of human caused mortality have been lower than the calculated PBR of 7533 the population has been classified as non-strategic (Gorbics et al.[5]). It is essential that harvest monitoring in both nations be maintained in order to accurately assess the impact of the harvest to this stock.

In summary, this new method of harvest estimation uses data from both harvest monitoring programs to account for interannual and intervillage variability in hunting success and applies a correction factor to adjust total harvest estimate to account for noncompliance with the MTRP. The accuracy of harvest estimates is therefore dependent upon the degree of hunter compliance with the MTRP rule. It is hoped that through ongoing information and education efforts that explain the importance of accurate harvest data, the understanding of and compliance with monitoring programs will improve.

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The trophic role of Atka mackerel, *Pleurogrammus monopterygius*, in the Aleutian Islands area

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Atka mackerel (*Pleurogrammus monopterygius*) is presently the most abundant marine fish species in the Aleutian Islands. Its exploitable biomass in 1998 was estimated to be 535,500 metric tons (t) (Lowe and Fritz[1]). The commercial catch of Atka mackerel increased from 26,740 t in 1991 to 104,000 t in 1996 (Lowe and Fritz[1]). Atka mackerel has been identified as food for other marine fishes, i.e. Pacific cod (*Gadus macrocephalus*) (Andriyashev, 1937), coho salmon (*Oncorhynchus kisutch*) (Wing, 1985; Volkov et al., 1995; Davis[2]), arrowtooth flounder (*Atheresthes stomias*) (Mito, 1974); sea birds such as thick-billed murres (*Uria lomvia*) (Ogi, 1980); and marine mammals such as Steller sea lions (*Eumetopias jubatus*) (Merrick et al., 1997). The western stock of Steller sea lions has recently been listed as endangered. A connection between the observed decline in Steller sea lions and the sea lion's dependence on commercially exploited fish species such as Atka mackerel as prey has been suggested (Merrick et al., 1997). Because of the great abundance of Atka mackerel and its important role as food for marine fish and marine mammals, it is essential to understand the trophic role of Atka mackerel in the Aleutian Islands area. The objective of this study was to describe the role of Atka mackerel as prey and as predator in the Aleutian Islands ecosystem.

Methods

Study area

From July to September 1991, the Resource Assessment and Conservation Engineering (RACE) Division at the Alaska Fisheries Science Center (AFSC), Seattle, Washington, conducted a groundfish resources trawl survey in the Aleutian Islands region. This area (Fig. 1) was divided into four major geographical units: southeastern Bering Sea area (from long. 165°W to 170°W, 42,604 km^2); eastern Aleutian area (long. 170°W to 177°W, 338,818 km^2); central Aleutian area (long. 177°W to 177°E, 322,234 km^2); and western Aleutian area (long. 177°E to 170°E, an area of 343,083 km^2). Two chartered fishing vessels, *Ocean Hope* and *Green Hope*, were used. Both vessels used standard RACE Division Poly-Nor'eastern, hard bottom, high-opening bottom trawls constructed of 12.7-cm (5-inch) stretched-mesh polyethylene web, with a 3.2-cm (1-1/4 inch) stretched-mesh nylon liner in the codend to retain smaller specimens (Harrison, 1993). Trawls were towed at 3 knots for 30 minutes. Scientists from the Resource Ecology and Fisheries Management (REFM) Division, Resource Ecology and Ecosystem Modeling Task, collected fish stomach samples during this survey.

Sample collection

Fish stomach samples were collected during trawling operations by scientists aboard the charter vessel *Green Hope*. Both Atka mackerel and their potential fish predators were sampled and measured, and stomach samples were collected. Because of the previously demonstrated high similarity (>60%) in diet between arrowtooth flounder and Kamchatka flounder (Yang and Livingston, 1986), no stomach samples of Kamchatka flounder were collected. Before excising a stomach, fish were examined for evidence of regurgitation or net feeding. If a fish had food in its mouth or around the gills, or if its stomach was everted or flaccid, the fish was categorized as having regurgitated food and the specimen was discarded. If a predator had fresh food (usually fish) sticking out of its mouth or throat, it was categorized as a net-feeding fish and was also discarded. When a sampled stomach was retained, it was put into a cloth stomach bag. A field tag with the species name, fork length (FL), and haul data (vessel, cruise, haul number, and specimen number) was also put into the bag. All of the samples collected were then preserved in buckets containing a 10% buffered formalin solution. When

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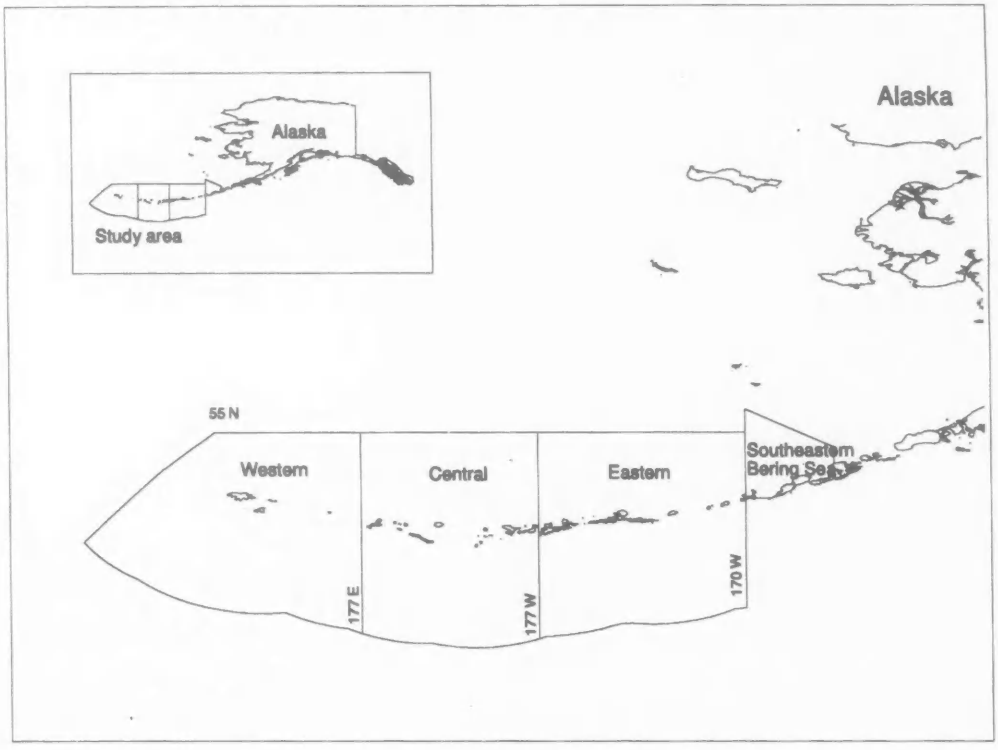

Figure 1
The subareas of the Aleutian Islands trawl survey area.

the samples arrived at the laboratory, they were transferred to 70% ethanol before the contents were analyzed.

Stomach content analysis

In the laboratory, stomach contents were first blotted with a paper towel and the wet weight recorded to the nearest one-tenth of a gram. After obtaining the total weight of the contents, these were placed in a petri dish and examined under a dissecting microscope. Each prey item was classified to the lowest practical taxonomic level. The numbers of noncommercially important prey were not counted; instead the percent total volume of these prey items in stomachs was visually estimated. Prey weights and numbers of commercially important crabs and fish were recorded. If walleye pollock otoliths were found, otolith lengths were measured and the pollock's standard length (SL) was derived through an otolith length-fish length regression table (from REFM's Ageing Task). Other fish otoliths were not treated as walleye pollock otoliths either because they were not found as frequently as walleye pollock or were difficult to identify to the species level. Standard lengths of prey fish, carapace widths (CW) of Tanner crabs (*Chionoecetes* spp.), and Korean horse-hair crabs (*Erimacrus isenbeckii*) were also recorded.

Data analysis

Atka mackerel as prey and predator The general diet of each species was analyzed to determine the overall percent total weight that each prey item represented in the stomach and to identify predators of Atka mackerel. Marine fishes that were mainly fish eaters were then selected for an analysis of population consumption of Atka mackerel. Stomach content analysis of Atka mackerel were performed to understand the role of Atka mackerel as a predator in the Aleutian Islands area.

Population level consumption of Atka mackerel by marine fish Following their identification as predators, the consumption of Atka mackerel by four marine fish species, Pacific cod, Pacific halibut, arrowtooth flounder, and Kamchatka flounder, was estimated. The amount of Atka mackerel consumed

at the population level was calculated by using the following equation:

$$\sum C_i = DR_i \times D \times B_i \times P_i,$$

where C_i = the consumption (by weight) of Atka mackerel by size group i of a predator species;

DR_i = the daily ration (as a proportion of body weight per day) of predator size group i (Table 1);

D = the number of days when Atka mackerel were vulnerable to predation (from 1 May to 30 September in this study);

B_i = the biomass of the predator size group i (Table 2); and

P_i = the proportion by weight of prey Atka mackerel in the diet of predator size group i (Table 3).

Daily rations were calculated by using annual growth increments and conversion efficiencies (Brett and Groves, 1979). Predator biomass data were obtained from the RACE Division database at the AFSC. The percent by weight of prey Atka mackerel in the diet of predators (P_i) was calculated for arrowtooth flounder, Pacific cod, and Pacific halibut. Because of the high similarity (>60%) between the diets of Kamchatka flounder and arrowtooth flounder (Yang and Livingston, 1986), the percent by weight of Atka mackerel that arrowtooth flounder consumed was also used for Kamchatka flounder.

Results

Atka mackerel as prey of marine fishes

Eleven commercially important groundfish species were collected: Pacific cod, *Gadus macrocephalus*; walleye pollock, *Theragra chalcogramma*; Pacific halibut, *Hippoglossus stenolepis*; arrowtooth flounder, *Atheresthes stomias*; Greenland turbot, *Reinhardtius hippoglossoides*; Atka mackerel, *Pleurogrammus monopterygius*; Pacific ocean perch, *Sebastes alutus*; northern rockfish, *S. aleutianus*; shortraker rockfish, *S. borealis*; and shortspine thornyhead, *Sebastolobus alascanus*. According to stomach content data, Atka mackerel (mostly juveniles) were found in the stomachs of Pacific cod, Pacific halibut, and arrowtooth flounder. The detailed food habits of these species were previously reported (Yang, 1996). The mean percent weights of Atka mackerel consumed by the predators are given in Table 3 by predator size and subarea. Arrowtooth flounder >40 cm FL consumed large amounts (36.6% by weight) of Atka mackerel in the western Aleutian area, whereas Pacific cod >60 cm FL and Pacific halibut (especially fish >80 cm FL) both consumed great amounts of Atka mackerel in the central Aleutian area (42% and 72.9% by weight, respectively).

Table 1

Daily ration (Dr_i, in terms of proportion of body weight per day) of four groundfish predators in the Aleutian Islands area in 1991.

Predator species	Predator size (cm)	Daily ration
Arrowtooth flounder and Kamchatka flounder	<20	0.009
	20–39	0.005
	≥40	0.008
Pacific cod	<30	0.011
	30–59	0.011
	≥60	0.008
Pacific halibut	50–79	0.004
	≥80	0.007

Atka mackerel as predator

A total of 238 Atka mackerel stomachs were analyzed, 231 (97%) of which contained food. Atka mackerel ranged from 22 to 44 cm FL, with a mean and SD of 33.5 cm and ±4.5 cm, respectively. Table 4 lists the percent by weight of the prey found in Atka mackerel stomachs. More than 90% of the total weight of stomach contents was invertebrates and less than 5% was fish. Euphausiids (mainly *Thysanoessa inermis*) were the most important prey, representing more than 28% of the total stomach contents. Calanoid copepods were another important prey of Atka mackerel, representing approximately 23% of the total stomach content weight. Larvaceans and *Themisto* sp., a hyperiid amphipod, occurred frequently but each represented less than 10% of the total weight of stomach contents. Squid were another invertebrate prey of Atka mackerel; they represented 5% of the total weight of stomach contents.

Several fish species were preyed on by Atka mackerel. Walleye pollock represented 2.4% by weight of the total stomach contents. Myctophids, bathylagids, zoarcids, stichaeids, and pleuronectids were also found. However, each of them represented less than 1% of the total weight of stomach contents. Cannibalism of eggs was also observed in Atka mackerel stomachs, and eggs represented 5.5% of the total weight of stomach contents.

Figure 2 shows the percentage by weight of the main prey items for different Atka mackerel size

Table 2

Biomass (B_i ; in tons) of predators of Atka mackerel by size groups in three subareas (W, C, E) around the Aleutian Islands and southeastern Bering Sea (SBS) in 1991. ATF = arrowtooth flounder; PCOD = Pacific cod; PH = Pacific halibut; ATKA = Atka mackerel; KF = Kamchatka flounder; W = western Aleutian; C = central Aleutian; E =eastern Aleutian.

Species (cm)	W	C	E	SBS	Total
ATF					
<20	1.9	0.6	29.4	37.6	
20–39	947.8	728.1	2162.1	4276.3	
≥40	3796.2	1571.1	4733.5	8315.8	
Total	4745.9	2299.8	6925.0	12,629.8	26,601
PCOD					
<30	12.5	153.7	138.6	151.6	
30–59	5507.2	9791.5	15,010.9	3886.2	
≥60	57,847.8	28,355.0	46,159.4	7448.3	
Total	63,367.6	38,300.2	61,308.8	11,486.1	174,463
PH					
<50	0	157.5	204.5	1857.8	
50–79	560.1	1795.1	6813.4	2891.8	
≥80	4745.9	5267.2	11,123.4	4207.9	
Total	5306.0	7219.8	18,141.3	8957.7	39,625
ATKA					
≤25	2537.9	2267.6	2000.0	0	
26–35	142,607.1	86,328.5	65,407.6	0	
>35	175,047.2	185,358.4	2629.7	0	
Total	320,192.3	273,954.5	70,037.4	0	664,184
KF					
<20	0	0	9.3	0	
20–39	280.9	251	442.2	4.8	
≥40	5281.5	9028.7	1114.6	881.7	
Total	5562.4	9279.7	1566.1	886.6	17,295

Table 3

Mean percent weight (P_i) of Atka mackerel consumed by marine fish in three subareas (W, C, E) around the Aleutian Islands and southeastern Bering Sea (SBS) in 1991. (—) indicates no sample. Values in parentheses are sample sizes. ATF = arrowtooth flounder; PCOD = Pacific cod; PH = Pacific halibut. W = western Aleutian; C = central Aleutian; E = eastern Aleutian.

Species (cm)		W	C	E	SBS
ATF	<20	—	—	0 (1)	0 (6)
	20–39	0 (20)	0 (9)	0 (56)	0 (36)
	≥40	36.6 (19)	0 (3)	0 (28)	14.3 (16)
	Total	32.1 (39)	0 (12)	0 (85)	7.1 (58)
PCOD	<30	—	—	0 (3)	0 (31)
	30–59	5.0 (78)	14.5 (44)	0 (68)	0 (28)
	≥60	25.3 (117)	41.7 (23)	5.6 (145)	0 (14)
	Total	24.1 (195)	40.2 (67)	3.6 (316)	0 (73)
PH	<50	0 (3)	0 (6)	0 (5)	0 (47)
	50–79	4.0 (10)	36.0 (7)	0 (39)	9.8 (33)
	≥80	38.5 (9)	72.9 (5)	0.2 (10)	0 (6)
	Total	28.2 (22)	33.8 (18)	0.1 (54)	4.0 (86)

groups. The most important food of the smallest (≤25 cm) size group of Atka mackerel were calanoid copepods (35% by weight) and larvaceans (33%). The most important prey of Atka mackerel between 26 and 35 cm FL were calanoid copepods (35%) and euphausiids (29%). The largest size group (>35 cm) of Atka mackerel consumed a substantial amount of calanoid copepods (18%), in addition to euphausiids (22%). Miscellaneous fish (walleye pollock, cottids, myctophids, and zoarcids) represented approximately 9% of the total weight of stomach contents of the largest size group of Atka mackerel. Atka mackerel eggs (as evidence of cannibalism) were found almost exclusively in the largest size group, representing 11% of total weight of stomach contents.

Walleye pollock were the most common fish species in the Atka mackerel diet. The size of walleye pollock consumed ranged from 49 to 63 mm SL with a mean and SD of 56.2 mm and ±4.8 mm, respectively. The cottids consumed by Atka mackerel ranged from 12 to 21 mm SL with mean and SD of 15.9 mm and ±3.1 mm, respectively. In addition, Atka mackerel stomach samples contained one bathylagid

Table 4

Mean percent total weight (%W) and mean percent of frequency of occurrence (%FO) of the prey items of Atka mackerel (*Pleurogrammus monoptgerygius*) collected in the Aleutian Islands area in 1991.

Prey name	%W	%FO	Prey name	%W	%FO
Polychaeta (worm)	0.62	2.59	Caridea (shrimp unidentified)	0.11	15.45
Gastropoda (snail)	0.88	34.86	Hippolytidae (shrimp)	0	0.48
Pteropoda	0.03	3.89	Pandalidae (shrimp)	0.12	0.32
Cephalopoda (squid and octopus)	0.07	5.29	Paguridae (hermit crab)	0	2.06
Teuthoidea (squid)	4.67	27.26	Majidae (spider crab)	0.06	3.81
Octopoda (octopus)	0.09	1.27	*Hyas* sp. (lyre crab)	0.02	3.66
Crustacea (unidentified)	4.89	6.98	*Chionoecetes* sp. (snow and Tanner crab)	0.06	6.72
Ostracoda (unidentified)	0.04	12.79	*Erimacrus isenbeckii* (Korean horse-hair crab)	0	0.32
Calanoida (copepod unidentified)	22.68	61.12	Cancridae (crab)	0.03	0.32
Eucalanidae (copepod)	0.23	5.49	Ectoprocta (bryozoan)	0.02	1.98
Eucalanus sp. (copepod)	0.01	1.29	Chaetognatha (arrow worm)	0.79	23.71
Pseudocalanus sp. (copepod)	0	0.34	Larvacea Copelata	9.05	72.28
Candacia columbiae (copepod)	0.51	45.00	Chondrichthyes	0.01	1.66
Mysidacea (mysid unidentified)	0.01	1.59	Osteichthyes Teleostei (bony fish unidentified)	0.1	1.27
Mysidacea Mysida (mysid)	0.01	0.63	Bathylagidae (deepsea smelts)	0	0.48
Acanthomysis pseudomacropsis (mysid)	0	0.48	Myctophidae (lanternfish)	0.75	0.95
Cumacea (cumacean unidentified)	0.02	5.29	*Theragra chalcogramma* (walleye pollock)	2.4	2.06
Amphipoda (amphipod unidentified)	0.02	1.82	Zoarcidae (eelpout)	0.67	0.32
Gammaridea (amphipod)	0.84	16.36	Atka mackerel eggs	5.52	6.67
Themisto sp. (amphipod)	2.41	59.16	Stichaeidae (prickleback)	0.01	0.32
Caprellidea (amphipod)	0.02	2.45	Pleuronectidae (flatfish)	0.01	0.32
Euphausiacea (euphausiid unidentified)	27.46	60.08	Unidentified organic material	10.39	28.49
Euphausia sp. (euphausiid)	0.03	0.48	Fishery discards	0.58	0.32
Euphausia pacifica (euphausiid)	0.02	0.48			
Thysanoessa inermis (euphausiid)	0.75	0.48	Total prey weight	700.55 g	
Thysanoessa inspinata (euphausiid)	0.14	0.32	Total nonempty stomachs	231	
Thysanoessa longipes (euphausiid)	0.1	0.48	Total empty stomachs	7	
Thysanoessa spinifera (euphausiid)	0.19	0.95	Total hauls	21	

(11 mm SL), one zoarcid (61.4 mm SL), one myctophid (59 mm SL), and one stichaeid (29 mm SL).

Consumption of Atka mackerel at the population level

The dominant predator species, Pacific cod and Pacific halibut, consumed large amounts of Atka mackerel (Table 5). The estimated amount of Atka mackerel consumed by each species varied by predator size as well as by the location where the predator was collected. For Pacific cod, large fish (≥60 cm) in the western and central Aleutian areas consumed between 14,000 and 18,000 t of Atka mackerel. For Pacific halibut, large fish (≥80 cm) consumed between 2000 and 4000 t in the western and central Aleutian Islands areas. Consumption of Atka mackerel by arrowtooth flounder was found in samples

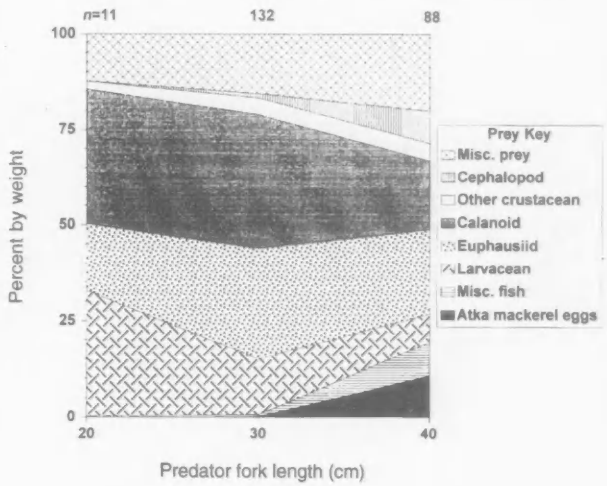

Figure 2

Variation in the main food items of Atka mackerel, by predator size, in the Aleutian Islands area in 1991. *n* = sample size.

Table 5

Biomass (t) of Atka mackerel population consumed by marine fishes in three subareas (W, C, E) around the Aleutian Islands and the southeastern Bering Sea (SBS) area in 1991. (—) indicates no sample. Values in parentheses are % total biomass. ATF = arrowtooth flounder; PCOD = Pacific cod; PH = Pacific halibut; KF = Kamchatka flounder. W = western Aleutian; C = central Aleutian; E = eastern Aleutian.

Species	(cm)	W	C	E	SBS	Total
ATF	<20	—	—	0	0	0
	20–39	0	0	0	0	0
	>40	1702 (3.5)	0	0	1455 (3.0)	3157 (6.5)
	Total	1702 (3.5)	0	0	1455 (3.0)	3157 (6.5)
PCOD	<30	—	—	0	0	0
	30–59	460 (1.0)	2394 (4.9)	0	0	2854 (5.9)
	≥60	17,914 (36.9)	14,487 (29.9)	3170 (6.5)	0	35,570 (73.3)
	Total	18,374 (37.9)	16,881 (34.8)	3170 (6.5)	0	38,424 (79.2)
PH	<50	0	0	0	0	0
	50–79	14 (0.1)	395 (0.8)	0	173 (0.4)	582 (1.2)
	≥80	1958 (4.0)	4114 (8.5)	19 (0.1)	0	6091 (12.6)
	Total	1972 (4.1)	4509 (9.3)	19 (0.1)	173 (0.4)	6673 (13.8)
KF	<20	—	—	0	0	0
	20-39	0	0	0	0	0
	≥40	126 (0.3)	0	0	154 (0.3)	280 (0.6)
	Total	126 (0.3)	0	0	154 (0.3)	280 (0.6)
	All species	22,173 (45.6)	21,390 (44.1)	3189 (6.6)	1782 (3.7)	48,534

from the western Aleutian and southeastern Bering Sea areas. Because the diet of arrowtooth flounder and Kamchatka flounder are very similar (Yang and Livingston, 1986), the daily ration values (Table 1) and the values of the mean percent of the Atka mackerel consumed by arrowtooth flounder (Table 3) were used for the calculation of the consumption of Atka mackerel by Kamchatka flounder. The total biomass of Atka mackerel consumed by the main marine fishes in the Aleutian Islands areas was 48,534 t (Table 5).

The number of Atka mackerel consumed by marine fishes was also estimated from the biomass consumed (Table 5) and the prey length recorded from stomach content analysis. The total number of Atka mackerel consumed by marine fishes in the Aleutian Islands area was about 284 million (Table 6), 84% of which were consumed by Pacific cod. The size and age composition of Atka mackerel consumed by groundfishes is listed in Table 7. Age-2 fish represented about 40% of the total numbers of Atka mackerel consumed by groundfishes, including predators of all sizes from different areas. Age-1 and age-3 fish accounted for 30% and 22% of the total numbers consumed, respectively. Age-0 Atka mackerel (4%) were consumed only by Pacific cod ≥60 cm FL in the central Aleutian area. Some age-4 and age-6 Atka mackerel were also found in marine fish stomachs, but they accounted for only about 4% of the total number consumed compared with about 25% of the Atka mackerel that were age 3. In terms of biomass, the age 2+ Atka mackerel consumed by marine fishes (41,071 t) represented about 3.2% of the estimated Atka mackerel population biomass (age 2+) (Lowe and Fritz[1]).

Discussion

Atka mackerel as prey of marine fishes

In addition to groundfish, such as Pacific halibut, Pacific cod, arrowtooth flounder, and Kamchatka flounder that feed on Atka mackerel, other marine fishes also consume Atka mackerel. Several authors have reported that pelagic salmonids prey on Atka mackerel. Davis[2] found that coho salmon (*Oncorhynchus kisutch*) ate Atka mackerel in the North Pacific Ocean. Volkov et al. (1995) found that Atka mackerel represented 30% and 13% of the food composition of coho salmon in the Sea of Okhotsk and the western Kamchatka areas, respectively. Gorbunova (1970) stated that 25–30 mm long larvae of Atka mackerel were found frequently in the stomachs of salmon caught in the open sea. In this study, no larval Atka mackerel were found in the stomachs of marine fishes, only juveniles or adults.

Table 6

Numbers (thousand) of Atka mackerel population consumed by marine fishes in three subareas (W, C, E) around the Aleutian Islands and the southeastern Bering Sea (SBS) in 1991. (—) indicates no data. Values in parentheses are % total numbers. ATF = arrowtooth flounder; PCOD = Pacific cod; PH = Pacific halibut; KF = Kamchatka flounder; W = western; C = central; E = eastern.

Species (cm)		W	C	E	SBS	Total
ATF	<20	—	—	0	0	0
	20–39	0	0	0	0	0
	>40	7217 (2.5)	0	0	9419 (3.3)	16,639 (5.9)
	Total	7217 (2.5)	0	0	9419 (3.3)	16,636 (5.9)
PCOD	<30	—	—	0	0	0
	30–59	3668 (1.3)	47,081 (16.6)	0	0	50,749 (17.9)
	≥60	75,358 (26.5)	113,249 (39.9)	0	0	188,607 (66.4)
	Total	79,026 (27.8)	160,330 (56.5)	0	0	239,356 (84.3)
PH	<50	0	0	0	0	0
	50–79	0	3390 (1.2)	0	0	3390 (1.2)
	≥80	6856 (2.4)	16,242 (5.7)	0	0	23,098 (8.1)
	Total	6856 (2.4)	19,632 (6.9)	0	0	26,488 (9.3)
KF[1]	<20	—	—	0	0	0
	20–39	0	0	0	0	0
	≥40	534 (0.2)	0	0	999 (0.4)	1533 (0.5)
	Total	534 (0.2)	0	0	999 (0.4)	1533 (0.5)
	All species	93,633 (33.0)	179,962 (63.4)	0	10,418 (3.7)	284,013

[1] I used ATF stomach content data and KF biomass.

Table 7

Numbers (thousand) by age (yr) and size (mm) of Atka mackerel consumed by the marine fishes in the Aleutian Islands area in 1991. ATF = arrowtooth flounder; KF = Kamchatka flounder; PH = Pacific halibut; COD = Pacific cod; w = western Aleutian; c = central Aleutian; sbs = southeastern Bering Sea.

Predator	Age 0 <131	Age 1 131–206	Age 2 207–261	Age 3 262–302	Age 4 303–333	Age 5 334–354	Age 6 355–370	Total
ATF≥40cm-w	0	0	4811	0	2406	0	0	7217
ATF≥40cm-sbs	0	0	9419	0	0	0	0	9419
KF≥40cm-sbs	0	0	999	0	0	0	0	999
KF≥40cm-w	0	0	356	0	178	0	0	534
PH≥80cm-c	0	0	8121	8121	0	0	0	16,242
PH5079cm-c	0	1130	2260	0	0	0	0	3390
PH≥80cm-w	0	0	3428	1714	0	0	1714	6856
COD30–59cm-c	0	47,081	0	0	0	0	0	47,081
COD30–59cm-w	0	0	3668	0	0	0	0	3668
COD≥60cm-w	0	7536	22,607	37,679	7536	0	0	75,358
COD≥60cm-c	11,325	28,312	50,962	22,650	0	0	0	113,249
Total	11,325	84,059	106,631	70,164	10,120	0	1714	284,013

Atka mackerel as predator

Atka mackerel have been documented as predators of both planktonic invertebrates and teleosts in both the western and central North Pacific Ocean. Simenstad et al. (1977) found that planktonic crustaceans, hyperiid amphipods, calanoid copepods, and oikopleura (larvaceans) occurred frequently in Atka

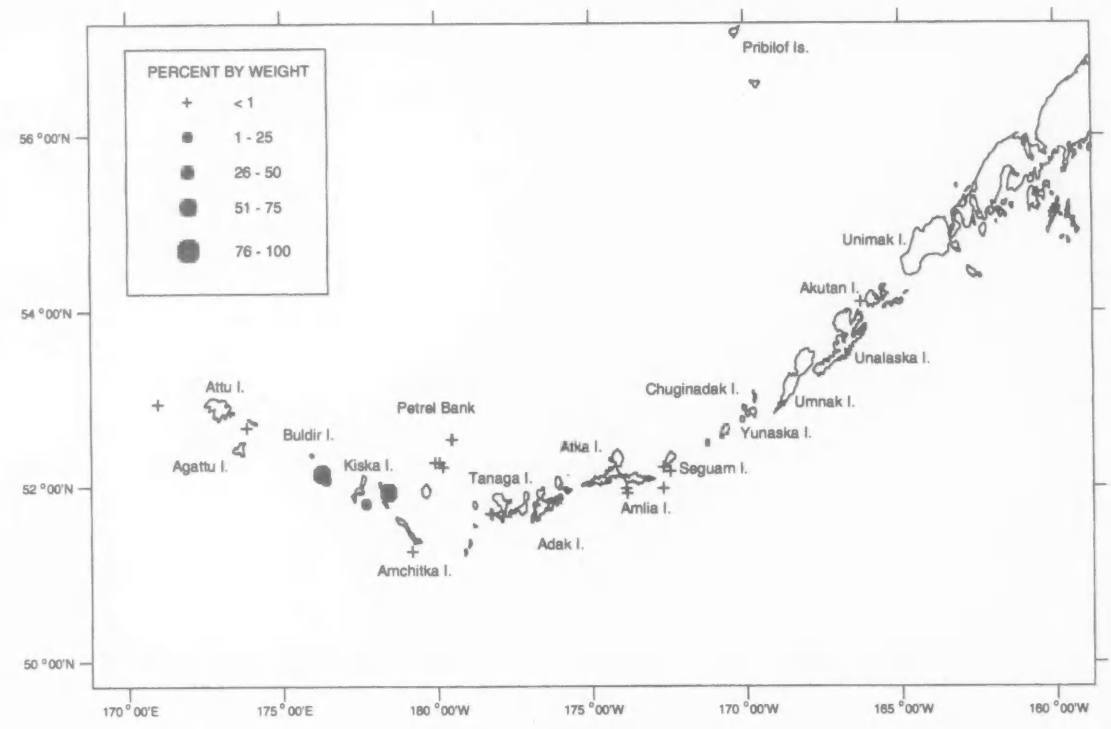

Figure 3

Geographic distribution of eggs cannibalized by Atka mackerel in the Aleutian Islands area in summer 1991.

mackerel stomachs collected from the Amchitka Island area. By contrast, in this study, euphausiids were the most important food (28% by weight). Onishchik (1997) found that myctophids (57% by weight) were the most important food of Atka mackerel in the Kuril Range area even though calanoid copepods and euphausiids occurred more frequently in stomachs. Orlov's study (1997) also showed that Atka mackerel is mainly a planktivore. He found that in the Kuril Islands area, copepods were present in 51% of Atka mackerel stomachs.

Several studies (Takemura and Yamane, 1953; Zolotov and Medveditsyna, 1979; Zolotov and Tokranov, 1991) have shown that Atka mackerel eat their own eggs. I also found evidence of egg cannibalism at four locations near Kiska Island (Fig. 3). I compared the frequency of occurrence of Atka mackerel eggs found at these locations. In three out of four hauls, females cannibalized more eggs than did males. In four hauls, males (n=7–9) exhibited 13–43% frequency of occurrence, and females (n=6–8) exhibited 17–57% frequency of occurrence of egg cannibalism. This finding suggests that male egg-guarding behavior, a characteristic of the species (Zolotov and Tokranov, 1991), may have inhibited the males from feeding on their own eggs. Combining stomach-content data from these four hauls (Table 8) showed that males consumed more euphausiids (27%) and less calanoids (18%), whereas females consumed more calanoids (35%) and less euphausiids (6%) when egg cannibalism occurred. I analyzed the rest of the data (where no egg cannibalism occurred) and found that males and females fed on very similar percentage by weights of calanoids (mainly (*Neocalanus plumchrus*)), euphausiids (mainly *Thysanoessa* spp), and larvaceans (Table 9). On the basis of these data, I hypothesize that egg-guarding behavior may cause some variations in diet of male and female Atka mackerel. All cannibalism occurred in September at depths between 80 and 170 m, indicating that the Kiska Island area may be a spawning ground for Atka mackerel in September. Zolotov and Tokranov (1991) found that, during the spawning season (from August to September), Atka mackerel eggs were the main food of rock mackerel (*Hexagrammos lagocephalus*), Atka mackerel, yellow Irish lord (*Hemilepidotus jordani*), and the common Irish lord (*H. gilberti*).

Table 8

Mean percent total weight (%W) and mean percent of frequency of occurrence (%FO) of the main prey groups of Atka mackerel (*Pleurogrammus monopterygius*) where egg cannibalism occurred in the Aleutian Islands area in 1991.

	Male		Female		Total	
Prey name	%W	%FO	%W	%FO	%W	%FO
Gastropoda (snail)	2.66	42.46	1.50	40.77	1.59	41.67
Teuthoidea (squid)	2.05	34.13	1.52	38.69	1.11	36.67
Calanoida (copepod)	18.54	66.02	34.89	77.83	21.30	71.67
Candacia columbiae (copepod)	0.98	49.06	0.80	52.23	0.74	51.67
Gammaridea (amphipod)	4.40	42.11	2.97	37.05	3.79	40.00
Themisto sp. (amphipod)	2.34	63.34	2.93	74.40	1.89	68.33
Euphausiacea (euphausiid)	27.23	49.16	6.14	42.26	19.42	46.47
Caridea (shrimp)	0.05	2.78	0.27	14.43	0.12	8.33
Majidae (spider crab)	0.48	8.68	0	0	0.20	5.00
Chaetognatha (arrow worm)	0.86	12.95	0.05	3.57	0.25	8.33
Larvacea Copelata	11.07	89.73	9.25	89.14	8.76	90.00
Gnathostomata	0.01	3.57	0	0	0.01	1.67
Zoarcidae (eelpout)	5.24	2.78	0	0	3.51	1.67
Pleurogrammus monopterygius (Atka mackerel eggs)	16.66	28.77	32.79	41.67	28.96	35.00
Fishery discards	3.92	3.57	0	0	3.05	1.67
Total prey weight	52 g		25 g		78 g	
Total nonempty stomachs	32		28		60	
Total empty stomachs	0		0		0	
Total hauls	4		4		4	

Table 9

Mean percent total weight (%W) and mean percent of frequency of occurrence (%FO) of the main prey groups of the Atka mackerel (*Pleurogrammus monoptgerygius*) that had no egg cannibalism in the Aleutian Islands area in 1991.

	Male		Female		Total	
Prey name	%W	%FO	%W	%FO	%W	%FO
Gastropoda (snail)	0.82	46.77	0.74	30.66	0.71	33.26
Teuthoidea (squid)	0.87	21.75	6.14	30.69	5.51	25.05
Calanoida (copepod)	30.02	60.81	22.08	60.20	23.01	58.63
Candacia columbiae (copepod)	0.32	41.52	0.53	48.36	0.46	43.43
Gammaridea (amphipod)	0.28	15.24	0.08	8.78	0.15	10.80
Themisto sp. (amphipod)	1.95	67.69	3.16	59.03	2.54	57.00
Euphausiacea (euphausiid)	26.78	63.40	31.81	68.63	30.86	63.24
Caridea (shrimp)	0.15	21.95	0.09	15.89	0.10	17.12
Majidae (spider crab)	0.03	4.04	0.05	4.37	0.03	3.53
Chaetognatha (arrow worm)	0.74	29.45	1.28	30.23	1.03	27.33
Larvacea Copelata	14.81	80.65	7.42	66.15	9.12	68.11
Gnathostomata	0.01	0.89	0.03	2.42	0.01	1.66
Myctophidae (lanternfish)	1.18	1.79	0.43	0.84	0.92	1.18
Theragra chalcogramma	2.79	2.81	4.12	2.86	2.96	2.55
Total prey weight	288 g		335 g		623 g	
Total nonempty stomachs	82		89		171	
Total empty stomachs	5		2		7	
Total hauls	14		17		17	

Atka mackerel as prey of marine mammals

Many marine mammals feed on Atka mackerel. Merrick (1995) found that Atka mackerel was the most common prey identified in Steller sea lion scats from the Aleutian Islands from 1990 to 1993. Nemoto (1957) found that Atka mackerel was the preferred food of humpback whales (*Megaptera novaeangliae*) in the waters west of the Attu Islands and the waters south of Amchitka Island. Kasamatsu and Tanaka (1992) stated that in the southwestern Hokkaido region, *Pleurogrammus azonus*, a congener distributed mainly in the northern part of the Sea of Japan, represented 80–100% of the diet of minke whale (*Balaenoptera acutorostrata*). Kenyon (1965) found that 85% (by volume) of the food of harbor seals (*Phoca vitulina*) in the Amchitka Islands area was Atka mackerel. Atka mackerel have also been found in the stomachs of sperm whales (*Physeter macrocephalus*) (Kawakami, 1980), killer whales (*Orcinus orca*) (Nishiwaki and Handa, 1958), fin whales (*Balaenoptera physalus*) (Nemoto, 1957), Dall's porpoise (*Phocoenoides dalli*) (Crawford, 1981; Perez and McAlister, 1993), minke whale (Perez and McAlister, 1993), harbor seal (Perez, 1990), northern fur seals (*Callorinus ursinus*) (Perez, 1990), and sea otters (*Enhydra lutris*) (Kenyon, 1969). Consumption of Atka mackerel at the population level by marine mammals was not estimated in this study because of insufficient data on their biomass, daily ration, and diet of marine mammals.

Atka mackerel as prey of seabirds

Seabirds are important predators in the Aleutian Islands marine ecosystem. Some seabirds feed on fish larvae or young juveniles, and some feed on zooplankton. Ogi (1980) analyzed the prey of 320 thick-billed murres (*Uria lomvia*) that drowned in Pacific salmon gill nets in the oceanic waters ranging from the Kuril Islands to a region east and south of the Aleutian Islands (160°W) and found that juvenile Atka mackerel and several species of lantern fish (Myctophidae) were important prey (17% of the total weight). Wehle (1983) found that Atka mackerel represented 42.3%, by occurrence, of the food of horned puffin (*Fratercula corniculata*), and it occurred in 6.3% of the stomachs of tufted puffin (*F. cirrhata*) at Buldir Island. Hatch and Sanger (1992) found only two Atka mackerel (138 and 139 mm) consumed by the tufted puffin, but Byrd et al.[3] found that Atka mackerel were important food of tufted puffin in 1990 at Buldir Island and Aiktak Island. Consumption of Atka mackerel at the population level by seabirds (like marine mammals) was not estimated in this study because of the lack of quantitative data on the biomass, daily ration, and diet of many seabirds in this area.

[3] Byrd, G. V., J. C. Williams, and R. Walder. 1992. Status and biology of the tufted puffin in the Aleutian Islands, Alaska, after a ban on salmon driftnets. U.S. Fish and Wildlife Service. Alaska Maritime National Wildlife Refuge. Aleutian Islands Unit, PSC 486, Box 5251, FPO AP 96506-5251, Adak, Alaska.

Summary

This study assessed the importance of Atka mackerel in the Aleutian Islands marine ecosystem. As a predator (mainly adults in this study), Atka mackerel were basically zooplanktivores. Calanoid copepods, euphausiids, planktonic tunicates, amphipods, and other crustaceans were principal food items. Atka mackerel also consumed some benthic fishes (cottids and young-of-the-year walleye pollock) and mesopelagic fishes (myctophids and bathylagids) and cannibalized its own eggs. As prey, about 48,500 t of Atka mackerel (mainly age 2+) were consumed by marine fishes. Table 7 indicates that about 26% of the consumed Atka mackerel were age-3 and older. Because of insufficient data, consumption of Atka mackerel at the population level by marine mammals and seabirds could not be estimated. Human beings also consumed a large amount of Atka mackerel. The total commercial catch of Atka mackerel was 26,740 t in 1991 (about 2.2% of the exploitable biomass [age 3+] in that year).

This study provides information about predator-prey relationships between Atka mackerel and their predators (marine fishes, marine mammals, and seabirds), and between Atka mackerel and their prey (zooplankton and other invertebrates) in the Aleutian Islands marine ecosystem. More information about the early life history (eggs, larvae, and juveniles) of Atka mackerel is needed to improve our understanding of their trophic role in the marine ecosystem.

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Ultrasonic telemetry: its application to coral reef fisheries research

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The importance to fisheries research of understanding movement patterns of fishes is increasingly being recognized (Hilborn and Walters, 1992). Traditionally, mark-recapture studies with external tags constituted the major method of examining movements in fishes (Shepherd, 1988). However, external tagging techniques are known to have several limitations (reviewed by Kearney, 1989) that often cannot be addressed adequately. In particular, data obtained through conventional tagging studies are usually limited to knowledge of a single point of capture, point of recapture, and the straight line distance and time interval between these two events. Such data can be misleading because the exact distance traveled and the patterns of movement are unknown. However, such patterns are of major importance to current research efforts in tropical reef fisheries, including investigations of spawning aggregation events (Samoilys and Squire, 1994; Zeller, 1998), and to the assessment of movements in relation to marine reserves (e.g. Russ and Alcala, 1996).

Ultrasonic telemetry is an ideal tool to address questions of movement and activity patterns of fishes. It can be used effectively under circumstances that limit the use of more traditional methods, yet its suitability for fisheries research is only slowly being realized (Nelson, 1990). Reviews of telemetry in the aquatic environment are provided by Harden-Jones and Arnold (1982), Hawkins and Urquhart (1983) and Nelson (1990).

Ultrasonic telemetry has been little used on coral reef fishes (e.g. Holland et al., 1993; Tulevech and Recksiek, 1994); most studies have concentrated on sharks (Nelson, 1990). Recent studies, however, have successfully applied the present techniques to the serranid *Plectropomus leopardus* (Zeller, 1997, 1998; Zeller and Russ, 1998), the primary target species of line fisheries on the Great Barrier Reef, Australia (Kailola et al., 1993).

The aims of this study were the assessment of ultrasonic telemetry in the coral reef environment and the application of the technique to *P. leopardus*. The first objective was the determination of a suitable transmitter placement technique and anesthetic. The second objective consisted of a field evaluation of ultrasonic telemetry. The final objective comprised tracking trials of *P. leopardus*.

Materials and methods

Study location and ultrasonic telemetry equipment

The study was conducted during 1993 at Lizard Island Research Station, northern Great Barrier Reef, Australia (lat. 14°40'S; long. 145° 28'E). The telemetry equipment consisted of V8-2L transmitters and a VR60 receiver linked to a directional 50–80 kHz hydrophone (Vemco Ltd, Halifax, Canada).

Evaluation of fish anesthetics and transmitter placement techniques

Fish (size range: 34.0 cm–52.5 cm fork length [FL]) were caught on hand lines. Aquarium facilities included 500-, 1000-, and 2000-L tanks with continuous flow-through water supply. Stocking densities did not exceed 2 fish/500 liters. Specimens were retained for an acclimation period (1–3 days), and were not fed for 24 hours prior to the experiments.

The first concern was that of procuring a successful, deep anesthesia that allowed a gentle recovery in the fish. Three anesthetics were tested: 1) Hypnodil™ (Janssen Pharmaceutica, active ingredient: metomidate) was used at a concentration of 7 mg/L (Mattson and Riple, 1989); 2) phenoxyethanol was used at a concentration of 0.5 ml/L (Mattson and Riple, 1989); and 3) MS-222 (tricaine methanesulfonate) was used at a concentration of 80 mg/L (Thomas and Robertson, 1991).

Three methods were used to attach telemetry units to the animals: 1) stomach placement (force feeding) by means of oral insertion of the transmitter into the stomach (e.g. Holland et al., 1992)—the least intrusive method, neither resulting in external protrusion of the unit, nor requiring surgery; 2) external placement by attaching transmitters directly to the dorsal musculature (Holland et al., 1996); and 3) internal placement by inserting transmitters into the body cavity as described by Hart and Summerfelt (1975) and Holland et al. (1993). Surgical implements were disinfected in ethanol and soaked in Tamodine™, a fish-antiseptic solution (Vetark Professional, Winches-

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ter, UK). The incision was placed parallel to the midventral line on the left hand side of the fish, 2 cm anterior to the anus and 1–2 cm lateral of the midventral line. Three to four rows of scales were removed from the area of planned incision, and the area was cleaned with Tamodine™. A 2–3 cm anterior-posterior incision was made into the body cavity. Disinfected transmitters were coated in antiseptic cream prior to careful insertion into the body cavity. The incision was closed with 6–8 surgical staples (Ethicon Proximate III™) as suggested by Mortensen (1990), the area was cleaned with Tamodine™, and the fish given an intraperitoneal injection of antibiotic (tetracycline 50 mg/kg of fish, McFarlane and Beamish, 1990), before being returned to the aquarium tanks.

Aquarium experiments Owing to limited aquarium space, it was not possible to evaluate all combinations of anesthetics and placement methods simultaneously. Hence two separate experiments were conducted. Experiment A examined the least intrusive transmitter placement technique (force feeding) with all three anesthetics. In experiment B the two intrusive techniques (external attachment and insertion into the body cavity) were tested in conjunction with the two most suitable anesthetics.

Experiment A: force feeding All three anesthetics were tested with force feeding to assess differences in retention times of transmitters due to the anesthetic agent. It was hypothesized that use of the hypnotic agent Hypnodil™ (metomidate) would result in the longest retention times owing to the low stress levels caused by this compound (Thomas and Robertson, 1991). *Plectropomus leopardus* regurgitate stomach contents easily, particularly when exposed to stressful conditions.[1]

Twenty-one specimens of *P. leopardus* (size range: 39.0 cm–52.5 cm FL) were assigned randomly to the three anesthetic treatments (n=7). Individual fish were anesthetized, tagged with T-bar anchor tags for identification, their fork length was measured, individually numbered transmitters were inserted into the stomach, and fish returned to the aquaria for recovery. Fish were fed daily. Aquaria were examined for regurgitated transmitters every two hours during daytime and once during the night. The start of each inspection was taken as the maximum retention period for any recovered units.

[1] Davies, C. 1992. Cooperative Research Centre for Reef Research, James Cook University of North Queensland, Townsville, 4811, Australia. Personal commun.

Experiment B: external attachment and surgical insertion The suppression of a stress response due to the use of metomidate (Hypnodil™) makes this a valuable drug for the routine handling of fishes (Thomas and Robertson, 1991). However, slightly elevated levels of the stress hormone corticosteroid are considered beneficial for resistance to trauma, thus making metomidate less suitable in situations involving stress, such as surgical procedures (Thomas and Robertson, 1991). Given the nature of the intrusive manipulations performed in experiment B, the use of Hypnodil™ was discontinued.

Experiment B compared two anesthetic agents (phenoxyethanol and MS-222) and two transmitter placement methods (external attachment and surgical insertion) in a full factorial design. The transmitter placement factor consisted of five treatment levels: external and internal placement treatments, external and internal placement controls, and a routine handling control. All fish received the same preliminary handling: fish were anesthetized, weighed (to the nearest 50 g), measured (fork length), and tagged externally. Routine-handling control fish were returned to the aquaria. The external attachment treatment consisted of attaching transmitters *sensu* Holland et al. (1996), and injecting an antibiotic intraperitoneally (tetracycline 50 mg/kg of fish, McFarlane and Beamish, 1990), before fish were returned to the aquarium. The procedure lasted 5–8 minutes. External-attachment control fish underwent the same procedure, but a transmitter was not attached after puncturing the musculature, and the fish were returned to the aquaria after eight minutes. The internal placement treatment consisted of surgical insertion of the transmitters into the body cavity as described above. The procedure took 15–20 minutes. Internal placement control fish were treated identically, but no transmitter was placed in the body cavity prior to closure of incisions. Fish were returned to the aquaria after 20 minutes.

Twenty *P. leopardus* were used (size range: 34.0–50.7 cm FL), resulting in two random replicates per treatment combination. Fish were fed daily, and each individual was examined visually without handling, to record general condition, behavior, feeding and wound status. The experiment was terminated after 24 days because gas-bubble-trauma (Weitkamp and Katz, 1980) affected the behavior (lethargy and cessation of feeding) of fish from all experimental groups. Upon termination, wounds were examined and classified as aggravated (ripped, or inflamed [secondary infection]), partially healed (40–50% wound closure), or healed (possibly minor inflammation). Subsequently, transmitters were removed and fish were weighed.

Data analysis Data from experiment A were analyzed for differences in retention times between anesthetic agents by using a single-factor analysis of covariance (ANCOVA). Fork length was used as a covariate to account for any effect of size of fish on the retention times. Assessment of experiment B was based on the observations made during and after the experiment. The change in weight during experiment B was analyzed by using a two-factor analysis of covariance (ANCOVA). Occurrence of gas-bubble-trauma was treated as a covariate. Underlying assumptions were evaluated prior to analyses (Sokal and Rohlf, 1981).

Field evaluation of ultrasonic telemetry in the coral reef environment

The extensive use of radio telemetry in wildlife research has produced procedures to assess the accuracy (bias and precision) of telemetry reception (White and Garrott, 1990). However, no such procedures appear to be published for ultrasonic telemetry. Given the paucity of studies with ultrasonic telemetry in the coral reef environment, a standardized field test using stationary transmitters was undertaken. Given that wind and sea-state influence the detectability of sound transmission in water (Jellyman et al., 1996), any effect of direction of prevailing wind on detectability or directional bias of observed sound signals needed to be assessed. Thus, the objectives of this field evaluation were 1) to establish the accuracy of directional bearings in relation to prevailing wind direction; 2) to evaluate observer bias and precision of bearings in relation to wind direction; and 3) to determine the optimal angle for cross-bearings, and the optimal distance between tracking boat and signal in order to obtain position estimates that minimize error polygons.

Experimental methods An ultrasonic transmitter (V8-2L, Vemco Ltd) was attached 15 cm above the substratum to a surface buoy in 4–6 m water depth. Three 200-m transects were run from the moored transmitter in relation to the prevailing wind direction:

0°: transmitter located directly upwind from any position on the transect.
45°: transmitter located at 45° downwind from the prevailing wind direction.
90°: transmitter located at right angle to the prevailing wind direction.

Marker buoys were positioned at 25-m intervals along each transect, starting at 50 m from the transmitter location (i.e. from 50 to 200 m), resulting in 21 positions for the three transects. Replicated compass bearings to the transmitter were obtained for each position by using the following protocol: the field of view of the observer was restricted to the tracking receiver for the duration of the experiment; an assistant anchored the boat at the marker buoys in random order and recorded the true compass bearing to the transmitter. The observer determined the perceived maximum directional signal strength by using the directional hydrophone. The corresponding compass bearing of the directional hydrophone (observed bearing) was recorded. The direction of the hydrophone was changed haphazardly by the assistant and the procedure was repeated. Six replicate bearings were taken at each of the seven distances on the three transects. The procedure was repeated by the second observer for a total of 252 observed bearings.

Data analysis Data were assessed for accuracy, bias, and precision (White and Garrott, 1990). Bearing error polygons were determined by using the largest and smallest directional bearing observed at each distance-marker buoy for any combination of two transects (0°–45°, 45°–90°, and 0°–90°). Thus, the error polygon parameters obtained (polygon area and maximum diagonal dimension) represented the largest possible error polygon estimates. Only bearing pairs from equidistant locations were used for polygon determination. Statistical analyses included Kruskal-Wallis nonparametric ANOVA and paired *t*-test. All data were examined for violations of underlying assumptions prior to analysis (Sokal and Rohlf, 1981) and data $\log_{10}$ transformed where applicable. Given that the angular scale of measurement represented only part of a circle, and absolute direction of angles was of no interest, data were treated as linear (Cain, 1989).

Field tracking trials

To verify the findings from the aquarium study, the two most suitable long-term transmitter placement techniques (external and internal placement) were tested under field conditions (MS-222 used as anesthetic). Two *P. leopardus* (43.1 cm and 58.9 cm FL) were equipped with external transmitters and released at their capture site after a 15-min recovery period. In the second field trial, internal transmitters were placed in two specimens (59.0 cm and 42.9 cm FL). Fish were released at the capture site after recovery from anesthesia.

The basic tracking technique described by Holland et al. (1985, 1992) was used. Exact positions of fish equipped with transmitters were determined by visual

triangulation (White and Garrot, 1990) by using identifiable landmarks and reef features. Triangulation involves the estimation of the location of a transmitter by using two or more directional bearings obtained from a known location (White and Garrot, 1990). Visual triangulation uses visible land and reef features that can be identified from maps or aerial photographs, in conjunction with directional bearings to identify the location of the transmitter.

Results

Evaluation of fish anesthetics and transmitter placement techniques

Experiment A: force feeding Gastric retention times of force-fed transmitters ranged from 18 to 216 hours; longer retention periods were documented for larger fish (Fig. 1, r=0.621, n=21). Mean retention times differed between anesthetic agents used (ANCOVA, $F_{2,17}$=4.762, P=0.023). The use of MS-222 resulted in a shorter retention time compared with either phenoxyethanol (SNK, P=0.004) or metomidate (SNK, P=0.001). Mean retention times did not differ with the use of either phenoxyethanol or metomidate (SNK, P=0.216). On average, fish anesthetized with MS-222 retained the transmitters for 42.0 hours (±9.7 SE), in contrast with fish anesthetized with phenoxyethanol (118.0 hours [±17.2 SE]) and metomidate (147.4 hours [±23.8 SE]).

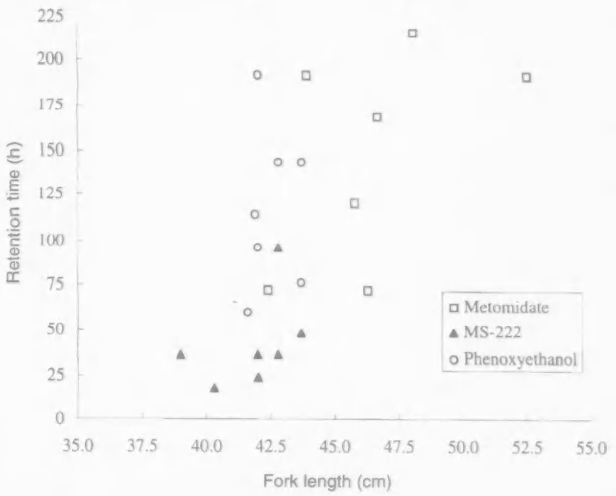

Figure 1

Correlation of gastric retention time of force-fed transmitters versus fork length of *P. leopardus*, as determined in experiment A (n=21, r=0.62). The three anesthetic agents are indicated.

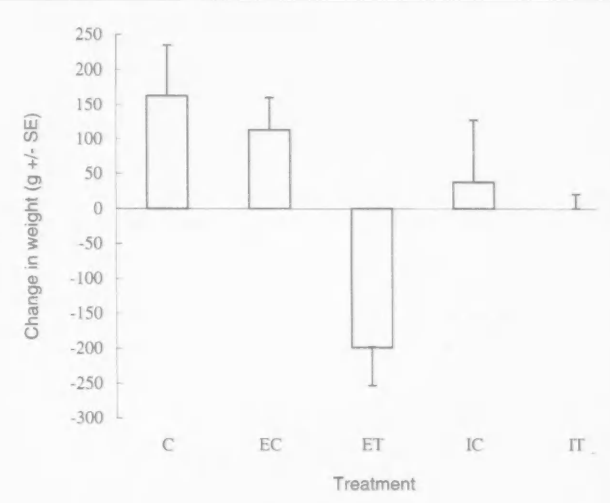

Figure 2

Change in mean weight (before treatment to after treatment) of *P. leopardus* as determined in experiment B. Note: negative weight indicates a loss in weight and vice versa. Presented are means (g ±SE). Treatments: C = routine handling control; EC = external attachment control; ET = external attachment treatment; IC = internal placement control; IT = internal placement treatment. n = 20.

Experiment B: external attachment and surgical insertion The change in weight of fish over the duration of the experiment differed significantly between transmitter placement treatments (ANCOVA, $F_{4,9}$= 5.309, P=0.018). Fish carrying external transmitters displayed a substantial reduction in weight compared with fish in all control groups that gained weight, whereas the internal treatment group showed no change in mean weight during the experiment (Fig. 2). Fish with external transmitters were observed spending a lot of time rubbing the attached transmitter against the substratum. Furthermore, most fish started feeding within two days, except for fish in the external treatment group and those anesthetized with phenoxyethanol in the internal control group (Table 1).

Table 1

Observations for aquarium experiment B. Treatment: C = routine handling control; EC = external attachment control; ET = external attachment treatment; IC = internal placement control; IT = internal placement treatment. Anesthetic: MS = MS-222; P = phenoxyethanol. "—" indicates that specimen never resumed feeding after treatment.

Treatment	Type of anesthetic	Level of anesthesia achieved	Day of first feeding	Affected by gas-bubble-trauma	Wound status
C	MS	deep	2	Y	—
C	MS	deep	2	N	—
C	P	twitching	2	N	—
C	P	deep	2	N	—
EC	MS	deep	—	Y	partially healed
EC	MS	deep	2	N	healed
EC	P	deep	—	Y	partially healed
EC	P	twitching	2	Y	healed
ET	MS	deep	10	Y	aggravated
ET	MS	deep	—	Y	aggravated
ET	P	deep	10	N	aggravated
ET	P	twitching	7	N	aggravated
IC	MS	deep	2	N	healed
IC	MS	deep	2	N	healed
IC	P	deep	7	Y	healed
IC	P	deep	7	N	healed
IT	MS	deep	2	N	healed
IT	MS	deep	2	N	healed
IT	P	deep	2	N	healed
IT	P	twitching	—	Y	healed

Observational records illustrated some differences in the effects of the anesthetics. All fish anesthetized with MS-222 attained deep anesthesia, whereas 40% of fish exposed to phenoxyethanol did not (Table 1). This resulted in twitching of the animal during treatment. Occasional cramp-like convulsions were also observed in some of these specimens during the early recovery period.

Examination of placement wounds after the termination of the experiment revealed consistent patterns (Table 1). The incisions made into the body cavities of internal control and internal treatment fish were healed (some minor inflammations did exist). The puncture wounds through the dorsal musculature of fish with externally attached transmitters were aggravated and in some cases enlarged due to repeated attempts to dislodge the transmitters. Wounds on external control fish were either healed or partially healed, and there were no further signs of aggravation.

Field evaluation of ultrasonic telemetry in the coral reef environment

Evaluation of bearing errors (true bearing-observed bearing) by transect (0°, 45° vs. 90°) indicated a significant difference in mean bearing error between transects (Kruskal-Wallis $H_{2,252}$=22.102, P= 0.000). The 90° transect displayed the least bias (mean=–1.50° ±0.7163° SE), the 0° transect had slightly larger, positive bias (mean=2.09° ±1.077°SE), and the 45° transect showed strong, negative bias (mean=–5.43° ±1.021°SE).

Owing to the differences in bias and accuracy between transects, observer differences in bias were examined separately for each transect. Bias differed between observers for the 0° transect (Kruskal-Wallis $H_{1,84}$=6.238, P=0.013); observer two showed positive bias compared with observer one (Fig. 3). Observers did not differ significantly in bias for the 45° transect (Kruskal-Wallis $H_{1,84}$=0.209, P=0.648, Fig. 3), or the 90° transect, (Kruskal-Wallis $H_{1,84}$=2.603, P=0.107, Fig. 3).

Paired t-tests were used to compare precision estimates (SD) between observers for each transect separately. No significant observer difference in precision was detected: 0° (t_6=1.2599, P=0.2545), 45° (t_6= 1.5819, P=0.1648) and 90° (t_6=0.6859, P=0.5184).

Evaluation of the parameters of maximum-error polygons indicated some clear patterns, both with respect to distance between sound source and tracking boat and with respect to angular combination of position bearings taken. The 0°–45° transect combina-

tion generally produced the largest error polygon area and length estimates, regardless of distance between sound source and tracking boat (Fig. 4). The 45°–90° transect combination produced similar results, with the exception of 50 m distance, where this combination resulted in the smallest polygon area and length (Fig. 4). Overall, however, the 0°–90° transect combination consistently resulted in the smallest polygon parameter estimates, irrespective of distance from which bearings were taken (Fig. 4). The best results for this angle combination were obtained at distances of 50 to 75 m from the sound source, with maximum-error polygon diameters of 58.5 m and 34.5 m, respectively.

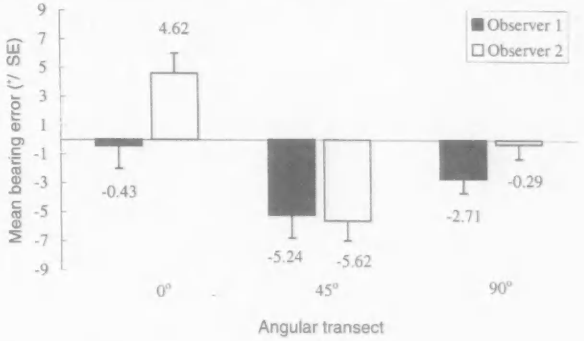

Figure 3

Mean bearing errors (±SE, n=42) for each observer on each angular transect, illustrating the difference in observed bias between the two observers for the transect facing directly into the prevailing wind (i.e. 0°). Mean values are indicated.

Field tracking trials

The two fish tagged with external transmitters did not travel far. The larger specimen traveled less than 25 m, whereas the smaller fish moved a maximum of 60 m. Both fish spent considerable time inside the shelter of the reef matrix, with the result that a low acoustic signal was received, accompanied by reduced reception angles. This behavior was confirmed during visual observations. The tracking trial was terminated after four days, and both fish were collected. Both specimens exhibited aggravated external wounds. Repeated dislodgment attempts, or snagging of the external transmitter on reef substratum had resulted in enlarged external wounds and loosened transmitters.

The two fish with surgically implanted transmitters took shelter inside the reef matrix immediately after release (observed on snorkel) and were not resighted. The signal weakened once the specimens had taken shelter, and remained weak for 48 hours. By the third day both signals were received strong and clear in the same location. Visual confirmation indicated that both transmitters were inside a whitetip reef shark (*Triaenodon obesus*). The immediate, postsurgery release of *P. leopardus* had resulted in mortality due to predation within 48–72 hours after release.

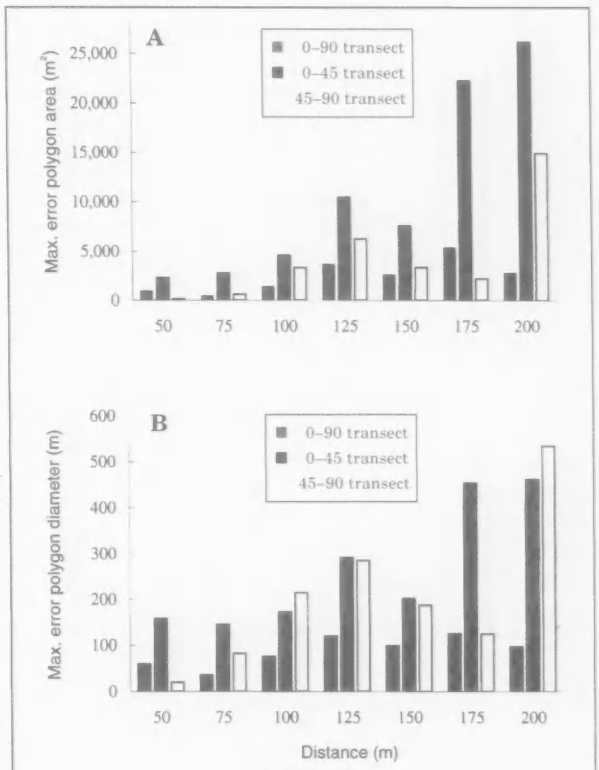

Figure 4

Maximum-error polygon parameters for each identical distance pair for the three possible angular transect combinations. Error polygons were calculated by using the largest and smallest angular bearings recorded from equidistant positions for each of the three possible angle combinations during the evaluation trials. Data pooled for observers. (**A**) Maximum error polygon area (m²). (**B**) Maximum diameter of error polygon (m).

Conclusions and recommendations

Transmitter placement and fish anesthetics

The aquarium experiments illustrated that, although surgical insertion is technically the most difficult method, it provided the least side effects

and should be selected for longer term studies, especially for bottom-associated reef fishes. Wound closure was observed within 14–21 days, and subsequent research (Zeller, 1997, 1998) illustrated that secondary infections were reduced with the use of a broad-spectrum bacteriacide (Myxazin™, Waterlife Research Industries, Longford, UK) and oral antibiotic (tertracycline). After the initial occurrence of gas-bubble-trauma (Weitkamp and Katz, 1980), the aquarium water was filtered through gravel prior to use. No further incidents of gas-bubble-trauma occurred (Zeller, 1997, 1998).

Releasing the experimental tracking specimens immediately after intrusive surgery meant releasing an injured fish that became a prime target for reef fish predators. All subsequent tracking specimens were retained for a recovery period in aquaria until the implant incision was healed (2–3 weeks). This procedure proved to be successful during subsequent studies and no further fatalities due to predation were observed (Zeller, 1997, 1998).

This study demonstrated clearly that external attachment of transmitters is not a viable option for *P. leopardus* because fish are disturbed by the external package and attempt to dislodge the devices. However, a study on a reef-associated carangid, a species with a more pelagic lifestyle, reported successful use of external transmitters (Holland et al., 1996). This finding illustrates the necessity of evaluating transmitter placement techniques in relation to species and species-specific habits.

Force feeding was demonstrated to be of use with *P. leopardus* only for short-term duration not exceeding a few days. Even the longest retention time recorded (216 hours) was considered unsatisfactory for longer term tracking studies (Zeller, 1997, 1998).

Tricaine methanesulfonate (MS-222) was the best anesthetic because it induced a successful loss of sensation and a gentle recovery, with the potential additional benefit of improved recovery from physical trauma because it elevated levels of the corticosteroid hormone (Thomas and Robertson, 1991). Furthermore, unlike with phenoxyethanol, Losey and Hugie (1994) did not observe any negative effects with MS-222 in regard to the olfactory sense. The present findings suggest that MS-222 represents the most suitable anesthetic for the surgical placement of transmitters.

Ultrasonic tracking of coral reef fishes

The following considerations will improve position estimation for tracking studies on coral reefs, and have been applied successfully (Zeller, 1997, 1998; Zeller and Russ, 1998): manual tracking with visual triangulation should be conducted by taking bearings at approximately right angles (90°) to each other and with approximate distances of 50–75 m between vessel and transmitter. Bearings taken at angles less than 90°, or taken at sharp angles to the prevailing wind, should be avoided. These considerations will result in minimal directional bias of bearings and ensure maximum accuracy and precision of estimates. If uncertainty about location or directionality of signal exists, it is suggested that "ground-zero tracking" (Nelson, 1990) be used to verify exact location of tracking specimen.

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Fishery Bulletin

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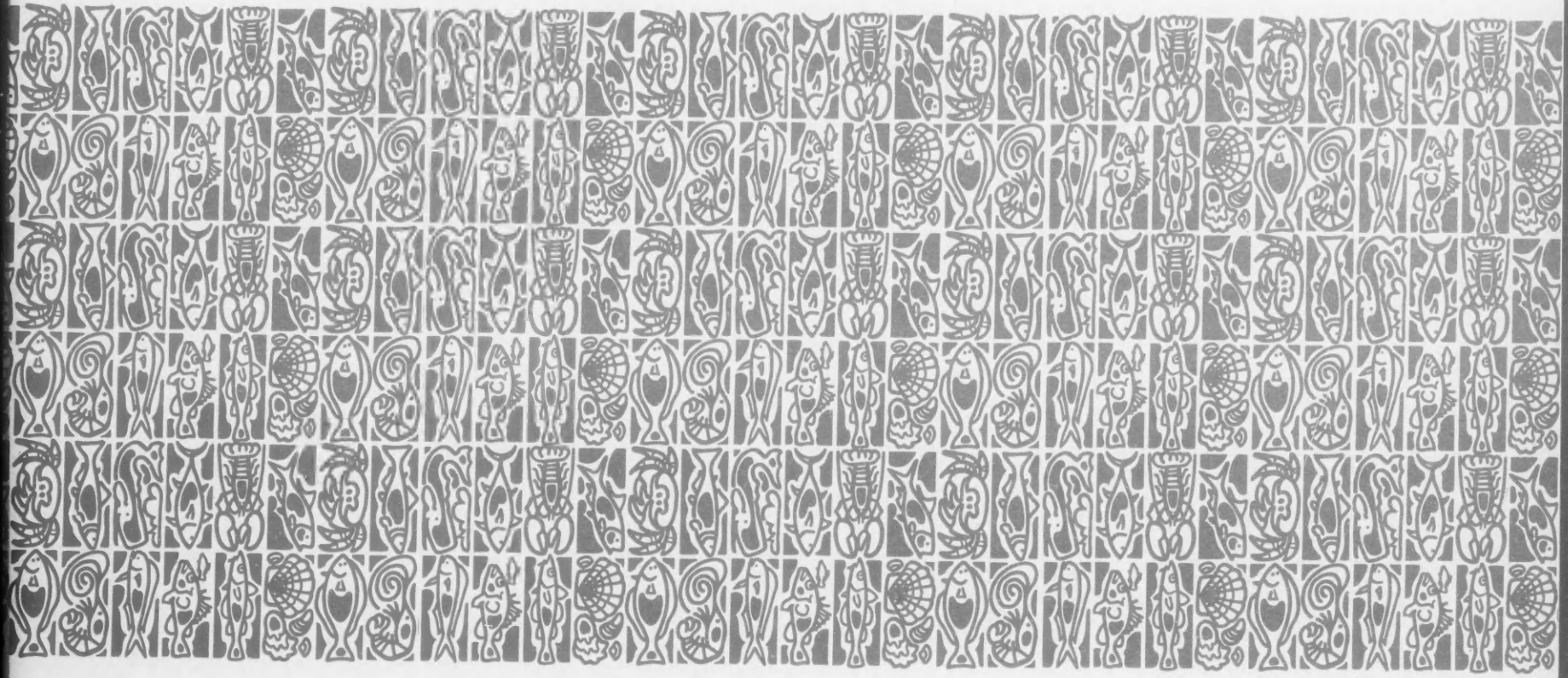

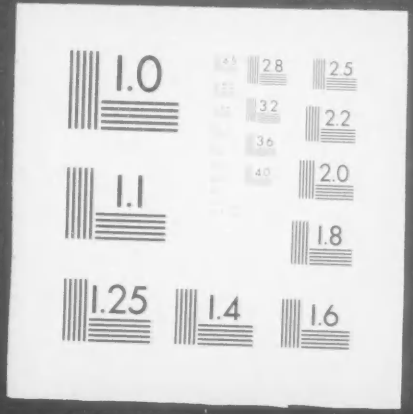
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